The Journal of HEREDITY

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The Gene and the Newcastle

Inheritance of Musical Memory

Long Petiolules and Short Metatarsals

Through The S. G. Chromosome with DNase and DNA

VOLUME 43 JANUARY-FEBRUARY, 1952 NUMBER 1

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The JOURNAL OF HEREDITY is published bi-monthly by the AMERICAN GENETIC ASSOCIATION at 32nd Street and Elm Avenue, Baltimore 11, Md., and 1507 M St., N. W., Washington 5, D. C. Address all communications regarding editorial matters to 1507 M St., N. W., Washington, D. C. Communications regarding the business management of **THE JOURNAL OF HEREDITY** may be addressed to the publication office, 32nd Street and Elm Avenue, Baltimore, Md., or to 1507 M St., N. W., Washington 5, D. C. Entered as second-class matter February 24, 1922, at the postoffice at Baltimore, Maryland. Acceptance for mailing at the special rate of postage provided for in section 1103, Act of October 3, 1917, authorized December 29, 1918.

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The

Journal of Heredity

Vol. XLIII JANUARY-FEBRUARY, 1952 No. 1

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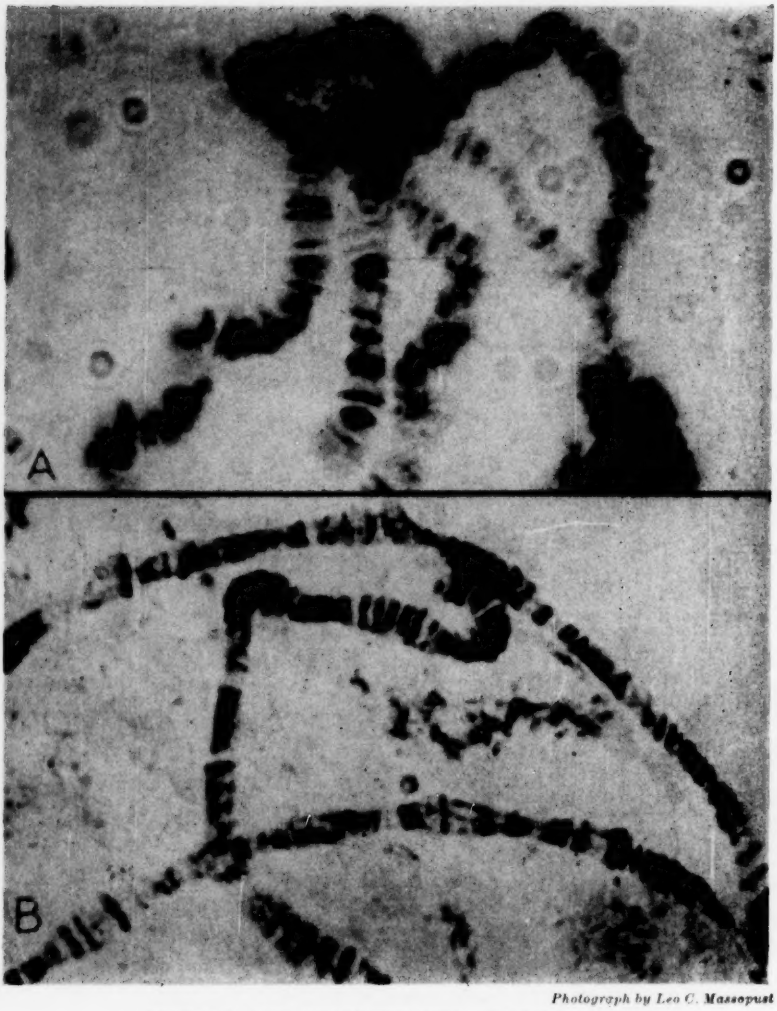

Photograph by Leo C. Massopust

CONTROL AND DNASE-TREATED CHROMOSOMES

Figure 1

A—Control chromosomes stained by the Feulgen technique. *B*—Chromosomes which had been treated with the enzyme, DNase, and then stained with brazilin. This treatment removes the desoxyribonucleic acid. Except for a possible reduction in the size and an increase in the discreteness of internal "structures" these chromosomes were optically identical with untreated controls.

STRUCTURE AND STAINING REACTIONS OF SALIVARY GLAND CHROMOSOMES

Of Drosophila Treated with Crystalline Desoxyribonuclease

E. S. McDonough, Mary Rowan, and Nancy Mohn

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THE salivary gland chromosomes of *Drosophila melanogaster* have been of much interest to geneticists since Painter[21] in 1933 pointed out their unique value in breeding experiments. Later he[22] and others allocated specific potentialities for development to definite chromosomal loci characterized by one or more "bands." The ultraviolet spectroscopy studies of Caspersson[4] and the use of the Feulgen technique by Heitz[10] and Bauer[1] early established that the bands of these giant chromosomes contained desoxyribonucleic acid. Since this substance has been shown to characterize chromosomes and to be related to gene action, much further work has been undertaken in regard to structure in relation to desoxyribonucleic acid (DNA). One phase of this work has had to do with the use of enzymes.

Studies on Chromosome Composition

Mazia and Jaeger[17] in 1939 immersed salivary glands for 22 hours in an extract from beef spleen and found that the chromosomes did not stain with aceto-carmine and there was no evidence of banding. The ninhydrin reaction was used to demonstrate that the chromosomes had not disintegrated. Two years later Mazia[15] reported that after treatment with beef spleen nucleases *Drosophila melanogaster* and *Sciara* chromosomes were Feulgen negative and the characteristic absorption spectrum of nucleic acid was not observed. Several other investigators have reported results obtained from studies in which crude nucleases were used on salivary gland chromosomes. Frolova[8,9] in her study of chromosome structure under enzyme treatment, reported extracts of both spleen and pancreas to result in negative Feulgen reactions but reported evidence of banding after treatment of *Chironomus plumosus* chromosomes. In 1942 Kodani[12] treated smears of chromosomes of *D. melanogaster* with beef spleen nucleases. He found the treated chromosomes to be Feulgen negative but the bands stainable with light-green. Catcheside and Holmes[5] used a highly purified desoxyribonuclease containing material prepared after the method of McCarty. These investigators reported that the banded regions were completely removed. Serra[25] found heterochromatic regions only of *Chironomous* to stain intensely with the Feulgen reaction after crude nuclease extract treatment. Palay and Claude[23] incubated smears of salivary glands of *D. melanogaster* and *D. pseudoobscura* with an extract from beef pancreas prepared as directed by McCarty. Formvar replicas were made of treated and untreated chromosomes so that the electron microscope could be used. The bands of the chromosomes were reported to be made up of small bodies which after digestion were more discrete, the bands being less dense.

The enzyme desoxyribonuclease (DNase), free from proteolytic and ribonuclease activities, crystallized and assayed by Dr. Michael Laskowski after the methods of Kunitz[13], was made available to the authors for study in 1949. A brief abstract of some results showing that enzyme treated chromosomes retained their microscopic structure was

published by McDonough and Rowan[18] in 1950. A more complete report as well as an account of new experiments and observations are presented in this paper.

Materials and Methods

The crystalline enzyme used in the experiments was stored in a deep-freeze. The stock solution was kept in the frozen state until needed. Since enzymatic activity was found to decrease appreciably after three hours at room temperature, all experiments were carried out within three hours after removal from the deep-freeze. For the first series of experiments in which the phase microscope was used the enzyme solution containing one microgram of crystalline DNase per ml. was in 0.2 M borate buffer pH 7, diluted to a molor concentration of 0.025 in respect to $MgSO_4$.

The chromosomes to be examined were obtained by placing fully grown larvae of *Drosophila melanogaster* in a drop of 50 percent glacial acetic acid. The salivary glands were then isolated under the dissecting microscope by means of glass needles. The glands were then transferred to a fresh drop of the acetic acid on a glass slide coated at least a day previously with a thin film of Bauer's albumin.[2] A coverslip was laid over the preparation and the glands were smeared by exerting slight pressure on the coverslip. Fixation was allowed to take place after which the coverslip was removed in distilled water and the smears washed in distilled water.

A measured amount (.2ml.) of the buffer and enzyme solution, which had been preheated beforehand to 37°C., was added to each slide and placed directly over the area of the smear. The slides were incubated at a constant temperature of 37°C. The humidity was kept at almost 100 percent by placing the slides in Petri dishes. The bottoms of the dishes were covered with distilled water and a triangle of glass tubing placed in the dish so as to keep the slides from coming in contact with the water. To prevent the water vapor, which condensed on the Petri dish cover, from dropping onto the slides and thus diluting the enzyme, a piece of absorbent filter paper was attached to the top of the dish. The incubation period was varied from one minute to 2 hours at times of one to ten minutes, 15, 20, 30, 45 minutes, one hour, and two hours. The slides for all the varied incubation periods were run in triplicate. Two control slides were run at the same time for each of the incubation periods. One control slide was treated with .2 ml. of buffer solution only and the other was treated with .2 ml. of buffer and boiled enzyme solution. At the end of the incubation period the enzyme and control materials were removed by washing thoroughly in distilled water.

Slides used in the staining experiments were prepared and manipulated as indicated above except that one hour after fixing in acetic acid the slides were placed erect in a coplin containing distilled water which just covered the cover slips. These were allowed to remain over night. Since it has been reported that buffers affect nucleic acids and their staining reactions, the DNase solution was prepared by placing one ml. of distilled water containing 100 gammas of the enzyme in one ml. 0.006 M. magnesium sulfate adjusted with 0.01N sodium hydroxide so that a pH of 6 was obtained in final solution. The .003 M. magnesium sulfate solution at pH 6 without the enzyme was used in controls. While maximum enzyme activity[13] is not obtained at pH 6 this was used in the experiments for sake of comparison of staining reactions with those obtained by others.[11]

One-half milliliter was used on each slide. In each run two control and two enzyme treated slides were incubated together at 37°C. and each experiment was repeated at least once. The usual procedure was to subject all four slides to the Feulgen technique and then to treat negative slides with other stains. At the same time slides taken directly after acetic fixation were stained.

The Feulgen technique used to determine DNase activity was modified after Bauer[2] and Heitz.[10] Experimentation showed that no fixation other than acetic acid was necessary if the time of hydrolysis was held very close to three minutes. The general plan of this schedule follows.

Chromosomes which had been smeared and treated, or not treated, as indicated above, were washed in distilled water and placed in a coplin of N/1 HCl suspended in a water bath with the temperature of the HCl kept at 60°C. The slides were allowed to remain for three minutes after which they were quickly removed from the acid and placed in decolorized[14] basic fuchsin at room temperature where they were allowed to remain for one hour. The smears were then rinsed in 50 percent glacial acetic acid and the acid removed by washing with 95 percent ethyl alcohol a drop at a time. The slides were mounted in euparal.

The brazilin staining method used was modified after the method followed by Belling.[3] Although a number of schedules were tried the following procedure gave clearest detail. Mordant in four percent aqueous ferric ammonium alum for 72 hours. Wash in 70 percent ethyl alcohol for 30 minutes. Stain in a ripe 0.5 percent solution of brazilin in 70 percent ethyl alcohol for three hours. Wash in 70 percent ethyl alcohol. Differentiate in four percent aqueous ferric ammonium alum for ten minutes. Wash in several grades of alcohol until absolute is reached. Clear in clove oil alcohol mixtures and xylol clove oil mixtures. Mount in balsam. Good preparations were

also obtained by mordanting over night in the ferric ammonium alum, rinsing in water, staining for one hour in the brazilin, rinsing in 70 percent alcohol, decolorizing briefly in the alum, dehydrating with 95 percent alcohol, and mounting in euparal.

Observations and Results

When smears which had been treated with DNase were examined with the ordinary light microscope it was found that the chromosomes, if treated for 15 minutes, were completely Feulgen negative. These Feulgen negative chromosomes did show evidence of banding. The control slides gave the characteristic Feulgen positive bands and colorless interband regions. The chromosomes which had been incubated with the enzyme for one through ten minutes showed a gradation in the staining capacities. Some of the DNA had apparently broken down even within one minute, for these briefly treated chromosomes were much lighter in color than the control for the same period of incubation time. From one minute on to ten minutes there was a definite gradation from violet to very light pink, while the control chromosomes were all violet.

When the phase microscope was used it was found that the bands which could just barely be seen with the light microscope stood out clearly. Enzyme treated chromosomes, both those which had been subjected to the Feulgen technique and those which had not, were similar in appearance. The banded regions were very apparent but were less dense than similar regions observed under the phase microscope in chromosomes which had been treated with buffer only, buffer and boiled enzyme, or untreated. The small bodies variously referred to as chromomeres, disk granules, etc. by other investigators, were observed in all slides studied. While objective tests were not available, they did, however, appear smaller and the material which surrounded them less dense in DNase treated bands.

Salivary gland smears kept in an incubator at 37°C. and degraded with DNase were found to be uniformly Feulgen negative. Control slides on which .003 M. $MgSO_4$ at pH 6 was placed when incubated at 37°C. were Feulgen positive (Figure 1*A*).

While a large number of staining techniques were applied to both treated and untreated chromosomes the results of the brazilin method have been of special interest. This stain revealed brownish-black, distinctly granular or "chromomeric" bands and four types of interband structure: a) clear areas which might have been caused by complete separation of adjacent bands or by the invisibility of fine connections; b) alveolar structure similar to that described by Metz[19]; c) "stress lines," very light in color, running diagonally across interband areas, apparently due to the stretching within the interband or to twisting of the entire chromosome; d) distinct, brown staining, longitudinal fibrils, or "chromonemata," connecting adjacent bands and very often connecting distinct, separate "chromomeres." While all these "structures" were distinctly visible with the ordinary light microscope in both DNase treated and untreated smears (Figure 1*B*) both bands and "chromomeres" did seem to be consistently lighter staining, smaller, and more discrete in the treated material. Iron haematoxylin was found to be similar to brazilin in staining capacity of both digested and undigested chromosomes but it was not found to be as effective as brazilin in differential staining of minute structure.

A number of other staining procedures were used in a preliminary way but only the most significant results have been presented here. Aceto-carmine which, as is well known, stains the bands of undigested material well, was found to stain the bands of DNase digested chromosomes slightly. Fast green which has been shown by Schultz[24] to stain the interband regions as well as the bands was observed to stain both bands and interbands following DNase with the bands at least as densely staining as those on slides stained with fast green but otherwise untreated. How this is be related to the releasing by nucleases of proteins to staining reactions as described by several investigators[11] should perhaps await further investigation. Methyl-green-pyronin[6] was found to stain the chromosome bands of controls an intense purple color with the interband regions little, if any, stained. Chromosomes degraded with DNase showed very light bluish-pink bands. An interesting staining reaction was observed when DNase alone in distilled water was used. Exposure to the enzyme for two hours resulted in chromosomes in which all but a few of the normally darker bands were Feulgen negative and unstained with methyl green. It was concluded that enough magnesium was present in the salivary gland cells to allow a slow degradation to take place.

Discussion

The results of the experiments reported in this paper would seem to indicate that the microscopic structure and general appearance of the salivary gland chromosomes of *Drosophila melanogaster* are not dependent upon the presence of desoxyribonucleic acid. It is to be remembered, however, that these chromosomes are unique in several respects and this should be taken into account in any generalization as to chromosome structure. There seems to be a general agreement[11, 16, 20] that chromosomes consist of

four main types of chemical compounds. These are ribonucleic acid, desoxyribonucleic acid, a basic protein of either a histone or a protamine type, and a tryptophane-containing protein. In regard to the relative importance of these materials in maintaining the microscopic structure there is, however, no general agreement. The recent work of Mirsky and Ris[20] indicates that the basic proteins (histone) may be removed from chromosomes isolated from liver, kidney, or pancreas and that the microscopic appearance remains unchanged. It was concluded from their experiments that the microscopic appearance of the chromosomes was due to an association of DNA with residual (tryptophane containing) protein, since, when histone-free chromosomes were treated with DNase, the only visible structures remaining were minute coiled threads of residual protein.

The results of the experiments on salivary chromosomes reported in this paper would seem to indicate that microscopic structure is maintained when DNA is removed, leaving residual and basic proteins as the chief components. It would thus seem that residual protein and either basic protein or DNA may together maintain the form and minute structure of the chromosome. Degradation with highly purified and crystallized DNase of chromosomes in all stages of the mitotic cycle and removal of histone without the removal of DNA or residual protein from salivary chromosomes should indicate the reliability of this statement as a generalization. Removal of "residual protein" only would be of great interest.

It is perhaps premature to consider the results of these experiments as regards the nature of the gene even in the light of the work of others. What would seem to be needed, judging from cytogenetic investigations, is the demonstration of a biochemical unit existing at the chromosome locus which assures, under ordinary conditions, the retention of the physiological potentialities and individuality of the locus through the generations and during such events as crossing over. It would seem logical that all of these four components commonly found in chromosomes play a part in the functioning unit. Which of them are responsible for individuation of the locus is another matter.

Summary

Salivary gland chromosomes of *Drosophila melanogaster* were treated with crystalline desoxyribonuclease free from proteolytic and ribonuclease activities. Studies of unstained slides examined with the phase microscope and also studies of material stained by a number of techniques showed that microscopic structure and general appearance of the chromosomes were not dependent upon the presence of desoxyribonucleic acid. Chromosomes treated with the enzyme were Feulgen negative, but were differentially stained with brazilin and iron haematoxylin. These results were considered in relation to chromosome structure and the nature of the gene.

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(Received August 15, 1951)

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POLYPLOIDY IN THE APPLE

Found Seven Years After Colchicine Treatment

Haig Dermen*

IN April 1942 six one-year-old apple trees of the varieties Baldwin, Delicious, McIntosh, Stayman and Winesap, were treated with colchicine. The technique used was essentially the same as that recommended for the pear[4]. Although polyploidy was detected in limited areas on some leaves during the first growing period following treatment, no branches were found on any tree where polyploidy could be detected. In the fall of 1942 the plants were taken out of the greenhouse and planted in the orchard.

In 1949, most of the trees bore fruits in moderate number for the first time. On one side of a McIntosh tree certain branches bore large, flattened fruits; of which some were smooth but most were irregular in shape, similar to "giant" fruits and quite typical of diploid-tetraploid periclinal sports of apple[1,5]. Cytohistological examination of a shoot tip from that region of the tree showed polyploidy in a chimeral form; the epidermis and the outer cortex (about six cells thick) of the stem were diploid and the remaining tissue was tetraploid. In this partial polyploidy the sex tissue in the flower remains normal diploid. Complete tetraploidy may be obtained from such chimeral polyploid material through adventitious budding technique[5,6].

Internal polyploidy in cranberry[2], peach[3], and pear[4] has been diagnosed with reasonable ease by characteristic changes in their leaves. In the apple this method is less successful because of the irregularities in shape and size of the leaves. Flowering and fruiting of the apple occur on older plants than in cranberry, peach and pear. These older apple trees are tall and the branches badly entangled. The trees were not pruned for fear of cutting off polyploid branches. Failure to recognize polyploidy at early stages of growth makes the problem of pruning difficult. As has been pointed out, changes in size of the flower parts, due to polyploidy, have not been very obvious in other plants mentioned. This is probably the case in the apple also, making visual detection of polyploidy through such small changes in the flower even more difficult.

Polyploidy in the apple can be detected most readily by three fruit criteria (Figure 2): (1) Increase in size (about twice the normal size); (2) flattened shape; (3) irregularity in contour. This is often due to internal diploid-tetraploid periclinal condition in parts of the affected tree. The flattened fruit shape, along with increase in size, has so far been the most useful criterion in the detection of induced or naturally occurring polyploidy in the apple.

The apple is the fourth fruit plant, that we have been able to polyploidize by colchicine treatment. This was more difficult than on

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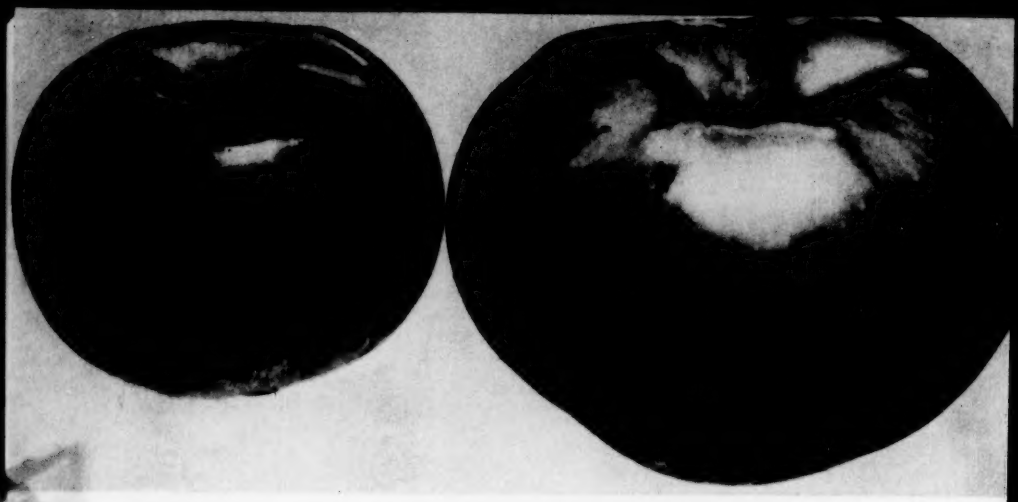

NORMAL AND GIANT McINTOSH

Figure 2

The fruits of "giant" sports of apple are quite commonly characterized by large size, flattended shape, and irregularity of contour. Natural size.

the cranberry, peach, and pear, and our results have been meager. The success reported here at least shows that colchicine can be effective in inducing polyploidy in the apple as in many other plants. However, to ensure success, a dozen or more trees of each variety may have to be treated; and a much longer period of time may be required before polyploidy in the apple can be detected and isolated. To facilitate earlier blooming and fruiting in the apple, it may be possible to put bud material to be treated in some dwarfing stocks.

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(Received October 24, 1950)

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A TETRAPLOID SPORT OF DELICIOUS APPLE FROM IDAHO

THANKS to Dr. Leif Verner of the Agricultural College, Moscow, Idaho, who sent us the material, we now have a large-fruited apple sport of the Delicious variety to be added to similar sports of McIntosh, Ontario, Wealthy, and Yellow Transparent varieties for breeding of tripolid and tetraploid sorts. A study of shoot tips from budded material of this new sport in April, 1950, showed it to be tetraploid in all internal tissues and diploid in the epidermis; therefore, it is sexually tetraploid and ready for breeding on polyploid levels.

In England a pear variety, Fertility, is known to be self-sterile; a tetraploid sport of it was found to be self-fruitful. The Delicious variety of apple is also known to be self-sterile; whether tetraploidy has made this variety self-fruitful, like the tetraploid sport of the Fertility variety pear, has yet to be determined.

Bureau of Plant Industry Haig Dermen
Beltsville, Md.

INHERITANCE OF FRUIT CHARACTERS IN THE STRAWBERRY

A Study of Several F_1 Hybrid and Inbred Populations

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IN breeding strawberries for fresh market purposes the characters which are constituents of external appearance are important. In this study the constituents of external appearance were considered to be external color, finish, size, uniformity, and shape of the aggregate fruit, position and color of the akenes. The expression of these characters and of flavor were studied by a rating system. An anaylsis of dominance, heterosis, and frequency of occurrence of characters was attempted on this basis. It was hoped that this and similar studies would be instrumental in reducing the breeding behavior of many important strawberry fruit characters to a statistical basis. With such data as a background it may eventually be possible to predict the frequency of occurrence of many fruit characters in certain strawberry breeding programs.

Powers[2] completed a similar study in 1945. He studied both plant and fruit characters. Certain of the fruit characters which he reported are the same as those which have been included here. The results obtained in each study in regard to these characters are in agreement even though the species and varieties involved were different.

Materials and Methods

The populations included in this study were handled in the same manner as all others of the strawberry breeding program of the University of California. Pollinations were made in the greenhouse during the late fall and winter. The seedlings were grown in the greenhouse during late winter and early spring and were transplanted to the field during the spring. The field planting was located in an area free of possible virus infection. The seedlings fruited during the spring and early summer of the year following the one in which they were transplanted. During the first picking season the characteristics of fruit from each seedling of the total progeny were studied.

Four hybrid populations and their respective inbred parental populations were included in this study. The hybrid populations were Banner × Blakemore, Banner × Klondike, Banner × Twentieth Century, and Klondike × Twentieth Century. The populations of inbred parents which were used were Banner selfed, Blakemore selfed, Klondike selfed, and Twentieth Century selfed. Only the F_1 populations of each hybrid and the first selfed generation of each inbred were studied.

Fruit notes were taken according to a rating system similar to that reported by Morrow, *et al.*,[1] and by Powers[2]. They were taken on fresh fruit samples from individual plants. The different characters were given numerical ratings of from 1 to 5. A rating of 1 indicated minimum expression of the character. A rating of 5 indicated maximum expression of the individual character.

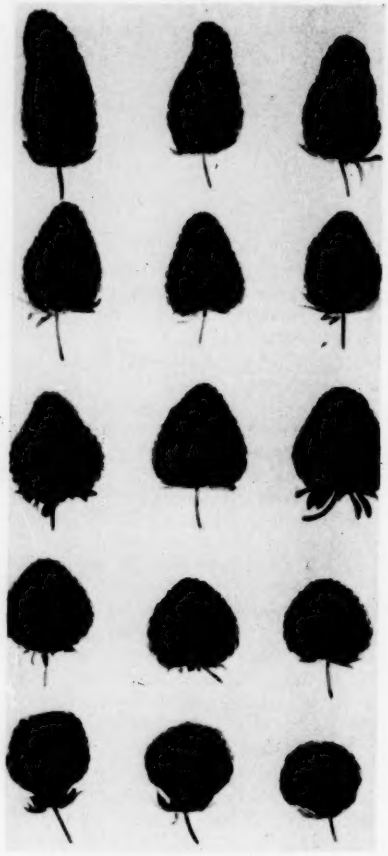
In botanical terms the strawberry is an aggregate fruit having many fruitlets embedded in the flesh of the receptacle at the surface and being exposed to varying degrees. The fruitlets are called akenes. In terms of common usage the aggregate fruit is called a fruit, a berry, or a strawberry, and the akenes are generally spoken of as "seeds." In the discussion which follows these terms of common usage have been substituted for botanical terms.

Ratings

Color was rated on the basis of intensity. A rating of 1 indicated insufficient red color, 3 was average and signified the most desirable color. Berries which were rated 5 for color were dark red. *Finish* was graded according to expression of a shiny or glossy surface. Dull fruit was rated 1; exceptionally shiny fruit was rated 5. *Flavor* was determined by testing several berries of each selection. It was recognized that personal likes and dis-

likes would differ widely; so a very general classification was used. All berries which had off-type or undesirable flavors were rated 1. The absence of any characteristic flavor was designated 2. A definite strawberry flavor, whether acid or sweet, was designated 3. Ratings of 4 and 5 were reserved for selections which had more intense, desirable strawberry flavors than those which rated only 3. Ratings for *size* were based on an average for each selection. The following scale was used: 1 = up to ¾" in diameter; 2 = ¾" to ⅞"; 3 = ⅞" to 1"; 4 = 1" to 1⅛"; 5 = 1⅛" to 1¼" or over. For *uniformity* a very rough type of berry was rated 1; exceptional uniformity was rated 5. The *seed position* of a selection was rated 1 if the seeds were set deeply in the flesh so that they were entirely below the surface. When the seeds were set flush with the surface, a rating of 3 was given. This was the most desirable seed position from the standpoint of appearance and ability to remain in good condition in the market. When the seeds protruded so that only the basal third or fourth of the seed was embedded in the flesh of the fruit, a rating of 5 was given. *Fruit shapes* of the various selections differed considerably (Figure 3). Oblate and round berries were rated 1, conic types were 3, and oblong berries were valued at 5 (Figure 3). Conic types were considered best in appearance. *Seed Color* varied from dark red, rated 1 through greenish 2, and yellow valued at 3. Lighter shades of yellow were designated 4 or 5. Yellow was considered to be a more desirable color than green or red. Although the ratings of 2 and 4 were not always mentioned in the above discussion, there was a progressive series from 1 to 5 for each fruit characteristic. In many cases the variation for a single sample was so great that a range of ratings was noted, such as 1-2, 2-3, 3-4, and 4-5. Thus there were actually nine evaluations which were used; 1, 1-2, 2, 2-3, 3, 3-4, 4, 4-5, and 5.

For statistical analysis of the frequency of occurrence of characters the ratings for each characteristic were grouped into two classes. The number for each class and percent in the more desirable class for each character was then calculated. These data are shown in Table II. The chi square method was used to test the significance of differences noted.



SHAPE RATING SCALE

Figure 3

Strawberries grouped according to the rating system used for shape. Top row oblong types rated 5; second row oblong-conic rated 4; third row conic rated 3; fourth row round-conic rated 2; bottom row oblate and round berries rated 1.

Results

Dominance and Heterosis

The means of the hybrids and the respective parents were compared for the study of dominance and heterosis. The two latter terms are used here to indicate different degrees of character expression in the hybrid over that of either parent. In the discussion which follows heterosis is used to refer to the phenotypic expression of a character in the hybrid when it has a value beyond the parental limits. Complete dominance is used to refer to the phenotypic expression of a character in the hybrid

when it has a value equal to that of either parent. Partial dominance is used when the phenotypic expression of a character in the hybrid population has a value which lies between that of the parents but is not equal to the midpoint between the two parents.

Good combining ability will be indicated by heterosis in the desired direction for all characters except external fruit color, fruit shape, and seed position. For these three characters good combining ability will be indicated if the hybrid population has a mean value approaching the most desirable class value (3.0).

The term "selfed" is used here to refer to the entire selfed populations of Banner, Blakemore, Klondike, and Twentieth Century. The term "hybrid" is used to refer to the entire populations of Banner × Blakemore, Banner × Klondike, Banner × Twentieth Century, and Klondike × Twentieth Century.

The means and standard errors of the populations for each character are given in Table I. The means of the hybrids and their respective parents as shown in this table are compared in Table II. The significance of each standard error of the difference for the four hybrids and their respective parents shown in Table II was tested by the chi square method.

The results for external *color* were inconclusive. Light color was dominant in the Banner × Blakemore hybrid but only partly dominant in the Banner × Klondike hybrid. The Banner × Twentieth Century hybrid showed no significant difference from either parent. The results for the Klondike × Twentieth Century hybrid were the reverse of those obtained for the first two hybrids in that dark color was dominant. Powers[2] obtained similar inconclusive results. These inconsistent data may be due in part to the difficulties involved in classification of color. The most desirable color would have a value of 3.0.

The information on *flavor* was incomplete and contradictory. In the Banner × Blakemore hybrid poor flavor showed partial dominance. In the Banner × Twentieth Century hybrid good flavor showed heterosis. The results are similar to those obtained by Powers[2]. Flavor appeared to be closely related to maturity. It is a character which results from a blend of sugars, acids, esters, and other substances. Even though one may have a keen sense of taste a more accurate or different method of analysis may be necessary.

The breeding behavior of the varieties tested in regard to finish, size, uniformity, and seed color is desirable and simplifies the task of the plant breeder. The results for the phenotypic expression of *size* were identical with those for *finish*. In every instance bright finish and large size showed heterosis. *Uniformity* showed either dominance or heterosis

TABLE I. Means and standard errors of the populations for each character.*

	Co	F	Fl	Sz	Un	Sd Po	Sh	Sd Co
Bs	2.8258	2.3652	2.3427	2.0281	2.0191	2.8820	2.6067	3.4326
	±.0693	±.0519	±.0374	±.0608	±.0416	±.0707	±.0787	±.0608
Bls	2.3613	2.5966	2.1429	2.0546	2.2647	2.6471	2.8950	3.0714
	±.0387	±.0346	±.0283	±.0490	±.0332	±.0548	±.0656	±.0387
Kls	2.4063	2.3125	———	1.7196	2.0938	2.7552	2.0260	3.8385
	±.0500	±.0361	———	±.0548	±.0400	±.0557	±.0480	±.0447
20 Cs	2.7250	2.1893	2.0036	1.9500	1.9786	3.4750	2.8929	3.6321
	±.0570	±.0384	±.0200	±.0480	±.0300	±.0424	±.0566	±.0678
B × Bl	2.3916	2.7817	2.2028	2.4458	2.2802	2.5526	3.0604	3.0635
	±.0245	±.0187	±.0141	±.0283	±.0245	±.0316	±.0490	±.0200
B × Kl	2.5494	2.8365	2.2341	2.7118	2.3247	2.1918	2.4776	3.1235
	±.0245	±.0173	±.0173	±.0283	±.0200	±.0224	±.0265	±.0141
B × 20 C	2.7619	2.9894	2.9127	2.5397	2.5688	2.7407	3.1710	3.0344
	±.0245	±.0100	±.0265	±.0400	±.0300	±.0346	±.0520	±.0100
Kl × 20 C	2.6118	2.9529	———	2.5470	2.7471	2.6824	3.0941	3.1353
	±.0400	±.0173	———	±.0574	±.0436	±.0529	±.0854	±.0245

*Key to symbols or letters used:

CO = Color; F = finish; Fl = flavor; Sz = size; Un = uniformity; Sd Po = seed position; Sh = shape; Sd Co = seed color.

Bs = Banner selfed; Bls = Blakemore selfed; Kls = Klondike selfed; 20 Cs = Twentieth Century selfed; B × Bl = Banner × Blakemore; B × Kl = Banner × Klondike; B × 20 C = Banner × Twentieth Century; Kl × 20 C = Klondike × Twentieth Century.

for uniform fruit. *Seed color* showed either dominance or heterosis for light color (yellowish).

The results for the phenotypic expression of *seed position* indicated dominance or heterosis for sunken seed position. Sunken seed position is probably more desirable than raised, but actually the most desirable type would have a rating of 3 and would be flush with the surface of the fruit. The Banner × Klondike hybrid had a low mean, indicating seeds sunken too deeply in the flesh of the fruit. Twentieth Century selfed had a higher mean value than any of the other populations.

The data for *shape* indicated that elongated shape may show dominance or heterosis. Elognated shape is less desirable than roundish to conical types, and the most desirable shape would be rated 3.0. From a plant breeding point of view the situation is similar to that of seed position. On this basis the analysis of the problem depends upon the frequency of occurrence of characters.

Frequency of Occurrence of Characters

All populations are classified in Table II according to the frequency of occurrence of characters. The number and percentage of individuals in the more desirable class for each character are shown. Chi square was used in testing the significance of differences between populations for each character.

Twentieth Century selfed and Banner selfed were darker in *color* than any of the other populations. The other populations did not differ significantly from one another. The Twentieth Century × Banner hybrid did not differ in color value from any of the other hybrids even though both parents were dark in color. None of the hybrid populations was exceedingly high or low in color regardless of the varieties used as parents.

The hybrids had higher values for *finish* than any of the selfed populations. The Klondike × Twentieth Century and the Banner × Twentieth Century had significantly higher values than the other two hybrids. Although Blakemore had a finish which was significantly brighter than that of any selfed population, its hybrid with the Banner variety ranked only third in value. Twentieth Century had a duller finish than any of the inbreds but showed good combining ability when crossed with Klondike or Banner.

The Banner × Twentieth Century hybrid had the best *flavor*. Banner selfed ranked next in value. Twentieth Century selfed had the lowest value. Therefore, the best hybrid

TABLE II. Significance of the Standard Error of the Difference for the Four Hybrids and the Respective Parents, Tested by the Chi Square Method.*

	Co	F	Fl	Sz	Un	Sd Po	Sh	Sd Co
Bs-B×Bl	**	**	**	**	**	**	**	**
Bls-B×Bl	0	**	0	**	0	0	*	0
Bs-B×Kl	**	**	**	**	**	**	0	**
Kls-B×Kl	-	**	—	**	**	**	**	**
Bs-B×20C	0	**	**	**	**	0	**	**
20Cs-B×20C	0	**	**	**	**	**	**	**
Kls-Kl×20C	**	**	—	**	**	0	**	**
20Cs-Klx20C	0	**	—	**	**	**	*	**

*A broken line indicates information incomplete or lacking; a zero indicates no significant difference; one asterisk means significance at the 5 percent level; two asterisks means significance at the 1 percent level. For explanation of letters used see Table I.

TABLE III. Classification of Populations Showing the Number and Percentage of Individuals in the More Desirable Class for Each Fruit Character.

	Bs*—891†		Bls—119		Kls—96		20 Cs—140	
	No.	%	No.	%	No.	%	No.	%
Co.	70	.7865	118	.9916	94	.9792	112	.8000
F	51	.5730	96	.8067	61	.6354	61	.4357
Fl	49	.5506	33	.2773			16	.1143
Sz	9	.1011	15	.1261	3	.0313	7	.0500
Un	24	.2697	55	.4622	32	.3333	15	.1071
Sd Po	54	.6067	81	.6807	62	.6458	27	.1929
Sh	64	.7191	70	.5882	96	1.000	83	.5929
Sd Co	47	.5281	89	.7479	6	.0625	49	.3500

	B×Bl*—323†		B × Kl—425		B × 20C—189		Kl × 20C—85	
	No.	%	No.	%	No.	%	No.	%
Co	322	.9969	411	.9671	188	.9947	85	1.000
F	302	.9350	393	.9247	189	1.000	85	1.000
Fl	125	.3870	165	.3882	177	.9365		
Sz	92	.2848	233	.5482	89	.4709	41	.4824
Un	163	.5046	224	.5271	141	.7460	74	.8706
Sd Po	244	.7554	387	.9106	122	.6455	58	.6824
Sh	175	.5418	344	.8094	56	.2963	41	.4824
Sd Co	270	.8359	343	.8071	176	.9312	62	.7294

*For explanation of letters used see Table I.
†Total number of individuals in the population.

resulted from crossing the best and poorest varieties. According to the rating system used, good flavor depended upon the combining ability of the varieties used.

The hybrids were significantly larger in fruit size than any of the selfed populations. Klondike selfed and Twentieth Century selfed were smaller in *size* than any of the other populations but the hybrid between these two varieties had the second largest value for size although it did not differ significantly from the Banner × Klondike or Banner × Twentieth Century hybrids. Apparently the Klondike and Twentieth Century varieties combined well with each other and with the Banner variety. The Banner selfed and Blakemore selfed had higher values than the other selfed populations, but the hybrid between these two varieties was significantly lower than any of the other hybrids. Poor combining ability is indicated.

The hybrids had better *uniformity* than any of the selfed populations except Blakemore. Klondike × Twentieth Century and Banner × Twentieth Century had better uniformity than any of the other populations, even though Twentieth Century selfed had the poorest uniformity. Good combining ability is indicated. The other hybrids and selfed populations had intermediate values for uniformity.

Of the selfed populations the Blakemore, Klondike, and Banner had significantly higher values for sunken *seed position* than Twentieth Century. Only the Banner × Klondike hybrid had a higher percentage of deep-seeded individuals than other populations indicating the significance of combining ability of the varieties used. Twentieth Century selfed was significantly lower than any other population, and Banner × Twentieth Century was significantly lower in value for sunken seed position than any of the hybrids. Since sunken seed position showed dominance or heterosis as indicated previously the hybrid population will equal or exceed the value of the parent having the more sunken seed position. Thus, the class values and the combining ability of the parental varieties must be considered in order to obtain a hybrid population having a mean value of 3.0, the most desirable seed position.

In regard to fruit *shape* Klondike selfed had the highest value for round to conical berries and differed significantly from all other populations in this respect. The Banner × Twentieth Century hybrid had a value indicating significantly longer berries than those of other populations. Although Banner selfed and Twentieth Century selfed did not differ significantly, when these two varieties were crossed with Klondike the resulting hybrids were different. The Banner × Klondike hybrid had a value indicating mostly roundish types while the Klondike × Twentieth Century hybrid was slightly longer than the preferred shape. Both hybrids approached the value of the parent having the larger percentage of elongated fruit shapes, but the actual percentage of the latter type in the hybrid progeny depended upon the parental varieties involved. The Banner × Blakemore and Klondike × Twentieth Century populations had mean values approaching the most desirable value of 3.0 (see Table I). This indicates good combining ability for the parental varieties involved.

Banner, Klondike, and Twentieth Century selfed had lower percentages for light *seed color* than any of the other populations. The Banner × Twentieth Century hybrid had a higher value than any of the populations. Klondike selfed had the lowest value and its hybrids ranked lower than others. The importance of combining ability and actual values of the parents is obvious.

Summary and Conclusions

Eight fruit characters were studied in four F_1 hybrid populations and four first generation selfed populations. Large *size* and *finish* showed heterosis in all instances. Dominance or heterosis was indicated for *uniformity* and light *seed color*. The results for *color* and *flavor* were inconclusive. It is likely that an analysis of the individual components of these characters will be necessary to obtain consistent results. Sunken *seed position* and elongated *shape* showed dominance or heterosis. For these two characters and for color, the most desirable phenotypic expression would have a value of 3.0.

A study of the frequency of occurrence of characters indicated that, except for external fruit color, a consideration of the combining ability of the varieties used was important in order to obtain the results desired. For fruit color the frequency of occurrence of characters showed significant differences among the selfed populations, but not among the hybrids.

In a strawberry breeding program the parents should have high values or good combining ability for large size, bright finish, good uniformity, and light seed color. This study indicated that the manner of inheritance of these characters is favorable to the plant breeder because in all cases dominance, or heterosis, of the desirable phenotypic expression of the character was indicated.

For the best seed position and fruit shape parents should be carefully selected to produce hybrid populations which will approach the value of 3.0 taking into consideration the fact that dominance or heterosis is indicated for sunken seed position and elongated shape.

The proper parental characters necessary to produce good color and flavor are indefinite.

More study of these characters is needed.

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(*Received October 29, 1951*)

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CASTLE ON INHERITANCE IN DOGS

PROFESSOR W. E. Castle has written a review of my book "Inheritance in Dogs, With Special Reference to Hunting Breeds," (*Journal of Heredity*, 42:150-51, 1951). It is only recently I have seen this review. I feel honored, indeed, that the distinguished American geneticist, whose knowledge of inheritance of coat color in rodents and other animals is unique, has shown in his 85th year such interest in my book which he finds "admirably suited for its purpose." I must admit, however, that I do not exactly appreciate Castle's statement that "from a scientific standpoint it is unfortunately confused." To this I must advance a mild protest. The account of the gene effects is not at all confused, and the result of every crossing is in full accordance with my descriptions of the gene effects, but it is true that these descriptions are not all in accordance with the descriptions of some other authors, for instance Little's, or with Castle's.

I have chosen a deviating description of the gene effect on certain points, partly, because the book is intended to be of assistance to practical breeders. A non-geneticist will understand more easily, that, when speaking of coat color, a *BBee*-dog is red, if *B* is described as a gene for red color than he will understand why the dog is red if *B* is said to be a gene for black color. And the breeder will find it easier to understand that a *bbEE* dog is liver when *E* is said to be a gene for liver-brown color than if *E* is described as a gene for extension of black or brown color.

Castle seems to altogether forget that there is not one gene description which is the only acceptable one. There may be several genes all leading to the same consequence. Thirty-two years ago I had the same discussion concerning coat color inheritance in horses. The three most common horse colors in Denmark are "red," "brown," and "black." Now, a "brown" horse is actually of the same color as a "red" one, the only difference being that the "brown" horse has black mane, tail and pastern.

I preferred in my text-book of genetics to describe the coat color variation in these horses as due to two genes: *S* = black; *ss* = absence of *S*; R = red. *rr* = absence of *R*. *S* + *R* give brown. We then have four types of brown—*SSRR*, *SSRr*, *SsRR*, and *SsRr*; two types of black—*SSrr* and *Ssrr*; and three types of red—*ssRR*, *ssRr*, and *rrss*. The last type is the entirely recessive red, not to be distinguished phenotypically from the other reds. It is easy to remember that animals with *S* only are black, with *R* only red and those with *S* + *R* are brown.

But of course it is possible, that physiologically a more probable description of the gene effect would be that *S* is a gene for black pigment, *ss* for red, and *R* is a gene for restriction of the *S*-effect to manes, tail and pastern, *rr* giving no restriction of the black color. But it is less pedagogic. Both theories would of course fit with experiences from practice.

As to the nose color in dogs I wrote in my book that, "It is necessary to have more extensive observations on nose color before its mode of inheritance can be clarified." It is not correct when Castle writes that my uncertainty is simply explained by the assignment of a wrong significance to the gene *B* (which he thinks will give a black nose). I have just discussed the possibility (page 61) of the gene *B* bringing about the black nose as proposed by Little, but I have furthermore mentioned that red dogs with brown nose are known. Whether the effect of *B* is described in one way or the other we are without an explanation for the existence of red dogs with a brown nose. In my opinion there is no clear-cut difference between black and brown noses, and this is just a point which makes the description of the *B*-gene as being a gene for black less acceptable. It is true that we know of cases in which a color-spot or the like, in a way, has fallen "outside" an animal, which according to its genetic formula ought to have shown it, but I do not like to describe an actually brown-nosed red dog as theoretically black-nosed. We must stick to the facts.

My book on dog genetics is not to be regarded as a scientific work but as a popular-scientific book written with the aim of making dog-breeders interested in the genetic side of their occupation.

Øjvind Winge

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HERITABILITY OF INTENSITY OF RED COLOR

In Hereford Cattle*

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HEREFORD cattle are red with characteristic markings known as the "Hereford pattern" which consists of a variable amount of white on the face, crest, underline, legs, and switch. The intensity of color varies from a very dark red to a dilute red frequently referred to as "yellow". This variation in intensity is continuous with no discrete color groups being apparent.

That intensity of color is somewhat heritable is shown by the trends in color which have accompanied changes in the color preference of breeders. In the 1920's, the preferred color of most western breeders was dark red, and considerable success was achieved in increasing the percentage of animals with this color[5]. During recent years the preference has been for a more "mellow" (medium-light-red) color accompanied by an evident shift of color in this direction.

Pitt[4] classified Herefords into two shades of color, "clarets" (dark reds) and "yellows" (light reds) and reported that clarets tended to breed true while clarets mated to yellows produced both clarets and yellows. No yellow matings were available for study. Pound[5] classified color in Herefords as dark red, medium red, or yellow red, and recorded the colors resulting from the six possible color combinations among parents. While no combinations of parents bred true for color, a study of the 406 matings recorded shows a regression of offspring on mid-parent score of 44 percent which is a direct estimate of the heritability observed. Hellstrom[2] reported heritability estimates of hair color of 63 percent based on the intra-sire regression of offspring on dam and 49 percent based on half-sib correlation.

Ibsen[3] and Shrode and Lush[6] have reviewed the information concerning the known genes which affect the intensity and dilution of color in cattle. The genes discussed do not appear to be responsible for the variation in intensity of red in Herefords.

The present study provides more information on the inheritance of color intensity in cattle.

Measurement of Intensity of Color

Intensity of color was scored by matching with a color standard derived by having an artist duplicate as closely as possible the color intensity of eight animals which were judged to divide the range in color into eight groups of equal range. The colors were mounted on a board and numbered from one to eight with the lightest shade of red being designated as one and the darkest as eight. Animals were scored for color by visually matching their color with one on that standard.

This method of scoring was simple and rapid. The repeatability of scores on an animal taken simultaneously by different people working independently was found to be 92 percent. The first year's scores were taken by using the modal score of a committee. Thereafter the score of one person was used.

Experimental Material

The records used in this study were from a herd of Hereford cattle owned by the New Mexico Experiment Station. From 1947

*Published with the approval of the Director of the New Mexico Agricultural Experiment Station as paper No. 63 in the Journal series.

†In cooperation with the Bureau of Animal Industry, United States Department of Agriculture and the state experiment stations under Western Regional Project W-1 on Beef Cattle Breeding Research.

through 1950, color scores were taken at weaning time from 437 weanling calves and their parents.

The records were first tabulated by sires and sex of calf and covariance analysis run for each year. Preliminary analysis showed that there was no difference in color scores of steer and heifer calves, however, so the sex classification was abandoned.

There was a slight but significant difference in both cow scores and calf scores during different years, apparently due to change in composition of the herd since the repeatability of scores on the same animal during successive years was 85 percent. There was some indication of change with age, however, since the calves consistently scored about one-half score darker than the cows. Also there was some indications that mature animals tended to score slightly higher during good years than during droughty years when the nutrition level was lower. Since these extraneous differences in years were small and the year classification resulted in no significant difference in heritability estimates, the data was classified finally by sire groups. The intra-sire regression of offspring on dam and regression of offspring on mid-parent score are shown in Tables I and II respectively. The progeny resulting from the various parental combinations are shown in Table III.

Heritability Estimates

The most reliable heritability estimates obtainable from this study were from the intra-sire regression of offspring on dam and regression of offspring on mid-parent score, which yielded estimates of 73.1 percent and 74.7 percent respectively. Estimates based on the intra-class correlation of calves by the same sire are of doubtful value since the variability of color in bulls was less than in cows and there was a tendency for dark bulls to be mated to light cows and vice versa. This selective mating was not deliberate and apparently resulted from avoiding closely related matings in a closed herd. The regression of sire-group means, adjusted for differences in average dam score, on score of sire was 0.42. This yielded a heritability estimate of 84 percent but only 16 bulls were involved and sampling error was large. Heritability estimated from the error of estimate intra-class correlation of half-sibs was 34 percent. The 95 percent fiducial limits of heritability estimate based on regression of calf score on mid-parent score were 60.5 and 88.9 percent. These estimates are slightly higher than those of Hellstrom[2].

From the relatively high heritability estimates, it would appear that intensity of color in this study was conditioned largely by genes with generally additive effects. Study of the individual matings involved (Table III) supports this suggestion. The offspring segregated around the mid-parent score, and in crosses of parents with opposite scores, there was no clear indication of dominance in either direction.

Number of Genes Involved

From the segregation which occurred, it would appear that there were approximately three heterozygous pairs of major genes involved. A fewer number than this should have resulted in more extremes appearing in the progeny of intermediate parents and it would be difficult to explain the number of extremes which did appear if more factors were involved. Additional genes exerting a small effect could also have been involved.

Discussion

High heritability of a character such as

TABLE I. Covariance analysis of color scores of dam (x) and scores of calf (y).

Source	df	Mean Squares and Products Dams	Calves	Cross Products	Errors of Estimate df	Mean Squares
Total	436	1.68	1.86	.66	435	1.62
Sires	15	1.60	3.53	—.33	15	5.20
Within Sires	421	1.89	1.77	.69	420	1.50

TABLE II. Regression of offspring score (y) on mid-parent score (x).

df	S_x^2	S_y^2	S_{xy}	Regression Coefficient
436	285	810	213	.747

TABLE III. The number and color scores of calves resulting from various color combinations of parents.

Score of Parents	Average Score of Parents	Score of Calves 1	2	3	4	5	6	7	8	Total Number of Calves	Average Score of Calves
1 × 3	2.0		2	2						4	2.5
1 × 4	2.5	1	3	4						8	2.4
2 × 3	2.5		1	2	3					6	2.8
3 × 3	3.0		3	7	3					13	3.0
4 × 2	3.0	1	7	6	16	1	1			32	3.4
5 × 1	3.0		1	1	3	1	2	1		9	4.6
3 × 4	3.5		3	20	24	10	4	1		62	3.9
5 × 2	3.5			4	7	1	1			13	3.9
6 × 1	3.5						1			1	6.0
3 × 5	4.0	1	4	4	10	6	7	2		34	4.3
4 × 4	4.0		3	13	26	26	10	4		82	4.5
6 × 2	4.0				1					1	4.0
4 × 5	4.5	2	1	2	32	10	14	7		68	4.7
6 × 3	4.5		1	1	3	3	3	2		13	4.9
7 × 4	4.5				3	1				4	4.3
3 × 7	5.0			2	1	2				5	4.0
4 × 6	5.0		1		7	7	5	3	1	24	5.2
5 × 5	5.0			2	9	4	3	3	1	22	5.0
3 × 8	5.5					2				2	5.0
4 × 7	5.5				4	3	7	1	1	16	5.5
5 × 6	5.5		1		2	4	5	1		13	5.2
5 × 7	6.0					1				1	5.0
6 × 6	6.0				1			1		2	5.5
5 × 8	6.5					1		1		2	6.0

color is not surprising. Since the character is not greatly influenced by external environmental conditions and there is no apparent reason why uterine environment should greatly influence it, genetic factors would appear to be largely responsible for variations in color. In this case, additive genetic factors apparently are in predominance.

It would be interesting to know why offspring from the matings with the more extreme mid-parent scores regressed toward the mean. Environmental effects, non-additive genes, inaccurate scaling of intensity which did not distinguish between the more extreme shades, and reduced effect of genes on either end of the scale rendering certain genotypes indistinguishable are possible explanations. It is possible that a more refined classification of color in this study would have yielded a higher heritability estimate.

Summary

Weanling Hereford calves and their parents were rated for intensity of red color by matching with a standard. Heritability of color was estimated from intra-sire regression of offspring on dam to be 73.1 percent and from regression on mid-parent to be 74.7 percent.

Segregation of progeny from various parental combinations suggested that approximately three pairs of additive genes determined intensity of red color in this study. No clear indication of dominance in either direction was noted.

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PLANT EMBRYOLOGY

PLANT Embryology* is a book which has been needed for some time; it is exhaustive, detailed, and accurate. This monograph has twenty-one chapters which may be divided, for convenience, into four sections: (1) An historical account of angiosperm and gymnosperm embryology, (2) Embryology of the Gymnosperms, (3) Embryology of the Anthophyta, and (4) Apomictic and Adventitious Embryogeny, and Polyembryony.

The history of embryogeny is divided into three epochs which are delimited by the appearance of certain fundamental publications. Epoch one begins in antiquity and ends with Hanstein's *Die Entwicklung des Keimes der Monokotylen und Dikotylen* in 1870. This paper also marks the beginning of the second epoch which witnessed the contributions of Kny, Solms-Laubach, Hegelmaier, Treub, Guignard, and others. Numerous "mediocre papers," appearing about 1910, marked the close of this epoch. The last epoch, subdivided into two periods, began with the contributions of Souèges. Souèges, according to Johansen, set the standard for embroyological work and in the whole of the last epoch (which is still in progress) only three embryologists approach him for excellence in embryological investigations. These are: Bhaduri of India, Crété of France, and Noll of Germany. Among other equally interesting facts, one learns that the first English embryologist to appear in this epoch is Metcalfe (1936); that German, Swedish, and Italian embryologists were (and still are) disposed towards the misuse of morphological terminology, and that Schnarf's *Embryologie der Angiospermen* and *Vergleichende Embryologie der Angiospermen* are inaccurately entitled.

In the second section, the Gymnosperms are divided into four phyla: Cycadophyta, Ginkgophyta, Coniferophyta, and Ephedrophyta. The first two phyla consist of one family each; the Coniferophyta lists ten, and the Ephedrophyta has three. In general, embryological treatment follows this order: (1) a brief statement about the family, the number of genera, and their embryological

**Plant Embryology*. Embryogeny of the Spermatophyta. Donald Alexander Johansen. xvi + 305 pp. Memoir edition, $6.00. Special edition, interleaved with writing paper and bound in half leather, $14.00. Chronica Botanica Company, Waltham, Massachusetts, and Stechert-Hafner, Inc., New York. 1951.

characteristics, (2) fertilization, (3) proembryo, and (4) embryo. Where a group is sufficiently known additional headings may appear as, for example, in the Pinaceae a section is devoted to "Comparative Embryology," or in the Sciadopitaceae the formation of "Bud and Twin Embryo" and "Rosette Embryos" is given. Good line drawings illustrate the text; some are redrawn from other authors and some are original. A short bibliography of the pertinent literature accompanies each family discussed.

The third section is concerned with the embryology of the Anthophyta. The author states that the "Anthophyta are treated as a unit, without segregation into the classical taxonomic groups, Dicotyledons and Monocotyledons." This is a noteworthy and commendable departure since the two groups cannot be separated satisfactorily on an embryological basis. The embryology of the Anthophyta is introduced by an account of the scope and definition of angiosperm embryology, early attempts at embryonomic classification, laws of embryonomy, types and variations, and finally a review and critique of the *Soužges' system of Classification*. Schnarf's system of designating types in embryonomic classification is adopted and improved. For example, Schnarf's *Asterecn-Typus* becomes *Asterad Type*. As may be seen, the suffix-*ad* is added to the root of the family name. In addition, each fundamental type is numbered: I Piperad, II Onagrad, III Asterad, IV Solonad, V Chenopodiad, and VI Caryophyllad. For the first time variations are included in embryonomic classification, for example, Solonad Type, Nicotiana Variation. There is a key to the six basic types and each type has a key to the variations within it. Five fundamental laws of embryonomy are given, namely: Parsimony, Origin, Numbers, Disposition, and Destination. An interesting series of formulae have been established (originally promulgated by Souegès), with additional symbols added by Johansen, which are especially useful in tables of comparison and recapitulation.

After the introduction to this section there follows "Special and Comparative Embryology," which begins with the Magnoliales and concludes with the Poales. The classificatory system follows that given in Hutchinson's *The Families of Flowering Plants*. The extent of the material covered may be indicated by the treatment of 105 orders and 184 families.

The last three chapters of the book are concerned with Apomictic Embryogeny, Adventitious Embryogeny, and Polyembryony. The text concludes with a special glossary (defining 98 terms peculiar to Embryology). There are indices to phyla, orders, and families; to genera and species, and to recapitulatory tables.

There is one error on page 269, line 16, where the species of *Eragrostis* cited should read "cilianensis" and not "chilensis."

This volume will do much to further the study of plant embryogeny and students of this highly specialized field will do well to heed Doctor Johansen's criticism of present investigations, namely: "(1) ignorance of the laws of embryogeny, (2) lack of thorough acquaintance with the publications of other investigators, (3) utter confusion in terminology, (4) failure to work out the proembryonomic development in sufficient detail, and (5) the solemn pronouncement of weirdly absurd conceptions of embryonomic relationships." Nearly all students of plant embryogeny will be pleased with this text. No embryologist should be without it.

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THE SOVIET VIOLATION OF BIOLOGY*

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OF all scientific subjects biology and especially genetics appears to be the branch of science with which authoritarian states most love to concern themselves. In the Third Reich, genetics was made to supply National Socialism with the ostensible scientific basis of its ominous race politics, and today the soviets are propagating in their own country and in all their satellite states including the soviet zone of Germany, a so-called "Soviet genetics," which is no less a pseudo-science than the racism of the Nazis. The methods which these authoritarian systems apply are similar, but the violation of our science has undoubtedly reached its most extreme development under the Soviets. There are no longer any inhibitions: scientific concepts are falsified entirely at will; statements which never were made are placed in the mouths of opponents; and viewpoints are ascribed to them which are often diametrically opposite to their actual ones. But what of it? No matter how bold the lie may be, the main thing is for it to be serviceable to Communist propaganda. A typical example has been selected below.

Recently an article entitled "The Science of Development from Lamarck to Lysenko," by the Soviet Russian A. N. Studitski†, was given mass-scale publication in German and distributed for a few East Zone pfennings apiece by the publishing house "Culture and Progress" (also two falsified concepts!). Herein, although in ostensibly scientific garb, rein is given to a wild diatribe against Mendelism, "the world view of reactionary clerical circles" as it is here called, and in the same way against "Morganism, the prop of the ideology of imperialism." Mendelian genetics, according to this, serves the purpose of justifying present-day imperialism, which is interested in propagating the idea of race differences, in establishing a scientific "basis" for race discrimination, in oppressing colonial countries, and in preparing a new war. It is further stated:

"According to Morganist 'science' race discrimination is biologically justified by the descent of Whites and Negroes from different species of apes. A leading American Morganist, Muller, says that danger of accumulation of harmful genes arises from the mixing of races. The prevalence of race prejudices in American bourgeois society is therefore not to be wondered at."

"The descent of Whites and Negroes from different species of apes"—what geneticist who is to be taken seriously has ever asserted this? Recently there was convened in Paris at the invitation of UNESCO a conference of leading anthropologists and geneticists, at which a declaration was adopted which begins with the words:

"There is general agreement in science that all human beings belong to the same species, *Homo sapiens*, and are derived from a common stock, even if opinions still differ concerning the time and the manner and means of the branching off of the different groups from this common stock."

All human races, even the most different ones, are fully fertile with one another. This complete fertility is the surest sign of their belonging to *one* species and being descended from *one* stock. The declaration of UNESCO also applies itself expressly against race

*Broadcast in German over RIAS in College Radio Program, October 16, 1951.

†Prof. A. N. Studitski is known to members of the American Genetic Association. His article, "Fly Lovers and Man Haters" was translated in the November 1949 issue of *The Journal of Heredity*. That article explains the genesis of the "different species of apes" idea.—ED.

discrimination as follows:

"The misuse of certain ideas concerning race for the purpose of race discrimination has occasioned serious human and social damage and in recent years demanded a high tribute in human lives. It is still continuing to hinder the development of many millions of people and their full participation in social life, and in consequence robs the world of the cooperation of potentially productive human forces."

As for the allegation on the Soviet side that the Nobel Prize winner, H. J. Muller, sees in the mixing of races danger of the accumulation of harmful genes, this too is an assertion purely for propaganda purposes, for the correctness of which no evidence at all is given or can be given. As Muller has recently pointed out with considerable emphasis, it is in the technologically most advanced peoples that the accumulation of detrimental genes is occurring and that the necessity arises for combating the increasing deterioration of the human biological heritage. This, however, has nothing at all to do with race crossing and race discrimination. On the contrary, people with primitive cultures, who are still in large measure under the influence of natural selection, are much less burdened with such detrimental genes than the people of advanced cultures, whose burdening with hereditary ailments is proportional to the degree of their cultural development. A primitive people living close to nature does not require eugenic measures for the combating of hereditary ailments.

Poultry Breeding à la Lysenko

So much for the article of Staditski's. But the Communist after-biology is propagated not only by brochures and books, the film too must be brought in. Again just one example. A film called "The Great Force" shows the breeding of a new race of poultry according to the system of Lysenko. In order to achieve a betterment of meat production the breeding method of Mendelian genetics, utilizing the crossing of appropriate races, is of course avoided—it is bourgeois and reactionary. But the Soviet genius who appears as a professor in this film has discovered the progressive method, which leads to the goal in the shortest time. He bores into the eggs of a race of poultry which has unsatisfactory meat production. How all this happens, how the shell of the egg is pierced and the substitution of albumin accomplished with the aid of a hypodermic needle, how the foreign albumin is injected and that proper to the egg itself flows off through other holes that were bored, is shown in the film in numerous pictures, designed to give it all a scientific aspect. It is of course to be understood that from an egg treated in this way the chicks which emerge have the desired characteristic. But will this characteristic be inherited as well? The work of the Soviet professor is no longer required to prove this, for in the film a simple peasant from a collective farm demonstrates the inheritance of the acquired characteristic, and thereby solves with the turn of his hand a problem on which numerous investigators had toiled in vain for a century. When one sees and hears all this, one presently questions whether some jester has not allowed a mockery of Lysenkoism to be shown here. But no, it must have been most earnestly intended. For in the journal "German Agriculture," issued by the Ministry of Agriculture of the Soviet Zone of Germany, this film is discussed in detail along with pictures taken from it, and it is proclaimed: "The film 'The Great Force' is a happy attempt to present the thoughts of Michurin and Lysenko in pictorial and lively form. The contest between the two world views is hereby brought clearly before one's eyes."

Two world views indeed—in place of light the Soviets seek to install darkness.

De Novo Cells

And what is Lysenko himself, the master mind of Soviet biology, now doing? His assertions are becoming ever more fantastic. He is no longer amusing himself with the transformation of winter wheats into summer wheats, and vice versa. He is now also having rye, oats and barley arise from wheat. The alleged discoveries of a Russian woman biologist, Olga Lepeshinskaya, provide, according to Lysenko, the explanation of these transformations of species. Lepeshinskaya has for nearly twenty years espoused the view that living cells can arise even out of unorganized albumin. She claims to have observed the origination of cells with nuclei, chromosomes and everything thereto appertaining out of, for example, egg white, and the detached yolk granules of the hen's egg. Lepeshinskaya has thereby returned to a view which in Western countries was held more than one hundred years ago, namely, that cells arise out of an organic mother liquor through "free cell formation." In the middle of the past century Rudolf Virchow had already shown the erroneousness of this proposition, and cell research since then has given an uninterrupted demonstration of the correctness of Virchow's expression *"omnis cellula e cellula,"* that every cell arises from a cell. Lepeshinskaya's contrary assertions completely lack foundation in fact and are taken with just as little seriousness by real Russian biologists as by those of other countries. How-

ever, Lysenko's confused ideas fit in excellently with Lepeshinskaya's. Let us see how he expresses himself about this in his newest publication, concerning "The Works of Olga Lepeshinskaya and the Transformation of Species":

"Within the plant body of a cereal organism there arise under the influence of appropriate conditions kernels of a rye body. But this origination does not take place by the transformation of the old into something new—in the given case by a wheat cell turning into a rye cell,—but by a process according to which, in the body of the organism of the species in question, kernels of the body of another species arise from material which does not possess any cell structure. Then out of these the cells and germs of another species are formed.

"It is this which the works of Olga Borisovan Lepeshinskaya provides us with, for working out a theory of the formation of species.

"Together with other achievements of science, the scientific theses won by Olga Lepeshinskaya constitute the fundament for the development of our Michurinist biology."

Thus Lysenko. One can no longer regard these fantasies otherwise than as products of a psychopathic mentality.

Such glaring nonsense is being disseminated today concerning biological and especially genetic matters, on command of the Soviets, that one may question whether it is worth while to expend even a word on it at all. If the nonsense were aimed only for the domestic use of the Soviets one might turn away from it in silence: it is not to be feared that it could fall on fruitful soil in Western civilized lands. However, the Soviet Zone of Germany too has to live on this miserable mental diet. We who have the good fortune to live in a free world should do everything within our power to bring adequate mental nourishment to our brothers in the Soviet Zone.*

*A stream of articles, letters and travellers' reports from all over the world show that the Lysenkoist propaganda is being taken with great and increasing seriousness by "intellectuals" in many countries not yet behind the Iron Curtain. This is true for example in India, the Middle East and South America, and even in Japan and some Western European countries. Thus the task of combatting this propaganda is one that really goes far beyond the Soviet Zone of Germany, to which the above article had originally been broadcast.—Ed.

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CONFERENCE ON USE OF ISOTOPES IN AGRICULTURE

KANSAS State College, Argonne National Laboratory and the Isotopes Division of the United States Atomic Energy Commission will sponsor a two-and-a-half-day conference on "The Use of Isotopes in Plant and Animal Research" June 12-14, 1952, at Kansas State College, Manhattan, Kansas. Persons wishing to receive a detailed program, together with information on housing, should write Director R. I. Throckmorton, Kansas Agricultural Experiment Station, Manhattan, Kansas.

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OAK RIDGE SYMPOSIUM ANNOUNCED

THE Fourth Annual Oak Ridge Summer Symposium, scheduled for August 25-29, 1952, will be sub-titled "The Role of Atomic Energy in Agricultural Research."

As contemplated, a number of sessions will be devoted to plant and animal studies with atomic energy research tools. Other lectures will deal specifically with Carbon-14 studies in both plants and animals.

The symposium is being given by the Oak Ridge Institute of Nuclear Studies and the Oak Ridge National Laboratory under the sponsorship of the University of Tennessee-Atomic Energy Commission Agricultural Research Program.

Additional information may be obtained from the University Relations Division of the Institute, P. O. Box 117, Oak Ridge, Tenn.

EVIDENCE FOR GENETIC VARIATION IN RESISTANCE TO NEWCASTLE DISEASE

In the Domestic Fowl

GEORGE F. GODFREY*

IT has been known for some time that there are genetic differences in resistance to such diseases as avian diphtheria, fowl typhoid, pullorum and lymphomatosis (Hutt,[3]). Recently it has been shown by Lerner *et al.*[4] that there is genetic variation in resistance to a respiratory infection in chickens tentatively diagnosed as atypical infectious coryza. The measure of resistance used by these workers was the ability of the birds in the available lines to maintain egg production during an epidemic.

The purpose of this paper is to report evidence for genetic variation in resistance to Newcastle disease, a virus disease which primarily affects the respiratory and nervous system of the fowl.

Description of Disease Outbreak

In November, 1949, an outbreak of Newcastle disease occurred on the Oklahoma Experiment Station Poultry Farm. The symptoms observed during this outbreak were typical of those described many times during the past few years (cf. Beach[1].) The first symptom noted was coughing and gasping. This was followed by lowered feed consumption and an abrupt decrease in egg production. A few birds exhibited muscular incoordination or partial paralysis. The onset of the disease was sudden and it spread rapidly. In spite of the fact that the affected birds were quartered in four different houses, all birds reached their respective low points in egg production within a fifteen-day period.

Postmortem examination of several birds by Experiment Station veterinarians revealed a cloudiness and yellowish thickening of the air sacs and a slight catarrh of the tracheae and bronchi. The virus causing the disease was not isolated and identified. Although such a procedure would have been highly desirable, the fact that two groups of birds had been previously vaccinated with a live virus vaccine and that these vaccinated birds showed no symptoms of the disease, seemed to be fairly conclusive evidence that the affected birds were suffering from Newcastle disease.

Materials and Methods

All birds considered in this analysis were pullets hatched during the spring of 1949. The hatching dates ranged from February 5 through April 30, so age differences of about eleven weeks are possible. However, as the majority of the pullets were hatched between February 21 and March 28, any age differences probably have little, if any, effect on the response of the birds to the disease outbreak.

The population of birds contained some breeds being developed primarily for meat production and others where the primary emphasis in breeding was on egg production. The A. and M. New Hampshires, White Plymouth Rocks, and Barred Plymouth Rocks are being developed for meat production while the remainder of the breeds and crosses are being developed and tested for egg production.

The ability of the birds to maintain production during the epidemic was used as a measure of resistance to the disease. A pause consisted of seven or more consecutive nonlaying days. All birds in pause before the disease outbreak were eliminated from the analysis, as were those which died during the outbreak.

Results and Discussion

The data in Table I show the average pause in days (with the standard error of the mean)

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and the mortality of the vaccinated controls and the affected birds. The difference in length of pause in egg production is highly significant, showing that Newcastle disease can be controlled by an adequate program of vaccination.

Among the unvaccinated or affected birds, the average length of pause varied from 17.3± 1.38 days for the White Plymouth Rocks to 37.8± 0.94 days for the A. and M. Strain of S. C. White Leghorns. An analysis of variance indicates that these differences in response to the disease are highly significant. As all of these breeds, strains and crosses were reared and maintained under the same environmental conditions, and had not been previously selected for resistance or susceptibility to Newcastle disease, it is highly probable that these differences are hereditary.

Rhode Island Red males mated to Barred Plymouth Rock females produced the Black-Cross pullets. Unfortunately the Reds were vaccinated and so constitute a missing link in determining the mode of inheritance of resistance to Newcastle disease. However, the mating of White Leghorn males (A and M. Strain) to Black-Cross pullets which produced the Three-Way Crosses provides evidence of the operation of multiple factors. The average pause of the Three-Way Cross pullets was between the parental range, although it tended to be somewhat nearer that of the Black-Cross females than the A. and M. White Leghorn females. From this fact one might speculate that some type of maternal influence, or some dominance of factors for resistance, as well as multiple factors, is involved in determining resistance to Newcastle disease.

It is possible that pullets laying at a high rate at the onset of the epidemic might be more severly affected than those laying at a low rate. Table II shows the rate of egg production for the various breeds, strains and crosses before, during and after the disease outbreak. By comparing these figures with the average pauses as shown in Table I, it can be seen that there was no consistent relationship between the severity of the disease and the rate of production at the onset of the epidemic.

An outbreak of this disease affected the flock the previous year, 1948. Most of the birds affected during 1949 were hatched from parental stock previously exposed, and thus natural selection could have played a part in determining the response of the 1949 pullets to the disease. It is interesting to note that the White Leghorns (RL) from the U.S.D.A. Regional Poultry Research Laboratory at East Lansing, Michigan, which have not been exposed to Newcastle disease, apparently have more resistance to the disease than the A. and M. Strain of Leghorns which have been previously exposed. Thus the demonstrated differences in resistance were probably due, for the most part, to chance differentiation of genotypes in non-interbreeding breeds and strains.

These facts demonstrating genetic variation in resistance to Newcastle disease are not in agreement with those of Dearstyne *et al.*[2], who found no differences in resistance to the disease among 12 sire families of the Rhode Island Red breed. The differences in the size and composition of the populations studied and the virulence of the causative organism could explain these divergent results.

Summary

The different response of various strains, breeds and crosses to a naturally occurring outbreak of Newcastle disease as measured by pauses in egg production indicates that there is genetic variation in resistance to the disease. Multiple factors seem to be involved in determining the degree of resistance or susceptibility to this disease.

TABLE I. Average Pause and Mortality of Birds Affected with Newcastle Disease Compared with Vaccinated Controls.

Breed, Strain, or Cross	No. Birds	Av. Pause days	Percent Mortality during outbreak
VACCINATED CONTROLS			
R. I. Reds	48	1.6 ± 0.64	5.9
New Hamp. (A&M)	125	6.5 ± 0.95	0
AFFECTED BIRDS			
W. P. Rocks	70	17.3 ± 1.38	6.2
Black-Cross Pullets*	43	18.3 ± 1.57	9.6
New Hamp. (A&M)	62	22.2 ± 1.65	4.6
Three-Way Crosses†	41	22.7 ± 1.90	5.9
New Hamp. (D)	86	23.4 ± 1.25	10.9
New Hamp. (W)	44	25.7 ± 1.41	7.7
W. Leg. (R. L.)	73	29.1 ± 1.62	13.4
B. P. Rocks	39	33.0 ± 1.63	2.6
W. Leg. (A&M)	74	37.8 ± 0.94	9.2

*Produced from mating R. I. Reds × B. P. Rocks.
†Produced from mating W. Leg. (A. & M.) × Black-Cross Pullets.

TABLE II. Percentage Egg Production Before, During and After Newcastle Disease Outbreak.

		Controls			Affected Birds								
		R. I. R.	N. H.	W. P. R.	Bl. X ♀♀	N. H. (A&M)	THREE WAY CROSS	N. H. (D)	N. H. (W)	W. L. (RL)	B. P. R.	W. L. (A&M)
Period												
Oct.	26-31	44	29	51	68	56	60	53	58	50	59	70
Nov.	1-5	53	38	18	74	51	65	6	13	56	65	67
	6-10	61	41	11	48	8	61	0	0	20	54	62
	11-15	60	51	16	12	2	25	1	2	0	42	19
	16-20	64	48	26	12	8	10	11	14	0	18	0
	21-25	59	48	44	26	16	11	26	31	1	0	0
	26-30	64	44	51	33	35	20	46	40	5	5	1
Dec.	1-5	68	42	56	48	44	35	48	51	25	9	6
	6-10	71	42	55	59	48	49	47	53	49	23	16
	11-15	73	43	42	65	43	49	50	51	60	31	42
	16-20	69	46	27	65	34	50	40	31	62	32	51
	21-25	67	51	29	70	34	52	35	28	56	39	50

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IDENTICAL TWINS DISCORDANT IN TONGUE-ROLLING

THE ability to turn up the lateral edges of the tongue, known as tongue rolling, is present in about 65 percent of the general population.* There are two distinct classes in regard to this ability, those able to roll their tongue are designated as positive, those lacking the trait being negative. Those individuals classified as positive are able to turn the lateral edges of the tongue completely up from the proximal end of the tongue distally about three-fourths of the total length of the tongue.

Rare cases of children have been found in which the ability may be acquired after considerable practice, although this factor is negligible. Data collected from a mixed population of 228 individuals indicate that tongue rolling has no relation to sex and that it shows a definite heritability.

It has been postulated that tongue rolling is simply inherited. If it is due solely to heredity, monozygotic twins would always be concordant for tongue rolling. It is the purpose of this investigation to determine the influence that heredity plays in the ability to roll the tongue. Over a period of two years, we have collected data from monozygotic twins in regard to tongue rolling. The usual criteria for diagnosis of monozygotic twins were employed. If there was any doubt as to monozygosity, the blood groups, the blood types, the finger and palm prints of the twins in question were compared. A total of 33 pairs of monozygotic twins, ranging in age from 10 years to 86 years, were classified. There were 25 pairs of monozygotic female twins and eight pairs of monozygotic male twins. This large numerical difference in sex can be explained by the fact that these data were collected at twin conventions which are attended in greater numbers by female twins than by male twins. The difference in sex number is of no consequence in this investigation as there appears to be no inter-sex alteration of heritability of this trait.

The number of concordant and discordant pairs observed are as follows:

	Male	Female	Total
No. of pairs both twins positive	5	13	18
No. of pairs both twins negative	1	7	8
No. of pairs positive and negative	2	5	7
	8	25	33

Of the total of 33 pairs there were 18 pairs of monozygotic twins who were positive and concordant for the trait, eight pairs who were negative and concordant, and seven pairs who were discordant. The percentage of discordant twins calculated from the data is 21.2 percent.

From the results of this investigation it must be concluded that tongue rolling is not entirely hereditary.

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*Sturtevant, A. H. *Proc. Nat. Acad. Sci.*, 26:100-102. 1940.

THE LINKAGE MAP OF THE TOMATO

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RECENT research with the tomato has made seed stocks available which are ideal for genetic class material, and research in developmental genetics. The importance of these stocks has not been appreciated by the geneticist. In bringing up to date the linkage map of this species, the possible genetic uses of this material are pointed out. The description of the various characters is brief, except in the cases where the points noted have not appeared in the literature, or where the points stressed have special significance. Where photographs of the character are available in the literature, the pertinent reference is included, along with the description of the character.

Seed Stocks for Genetic Classes and Research in Developmental Genetics.

The genes with high expressivity that are easily identified and are best for beginners or class material, are marked in the list presented on pp. 26 to 34 with an asterisk. As a laboratory exercise for genetic classes, the seed from appropriate crosses are planted four months before the material is needed. The students harvest the ripe fruit, spread the seed on paper to dry, and then plant them a few days later. This procedure enables the student to observe the phenotype of the F_1 plant, and to know that the seed all came from one plant, thus avoiding the misconception that he is dealing with selected material or a mixture of seeds of different parentage. The seed can be planted fairly thickly in rows either in flats or bench beds. As many as 200 plants to the square foot can be raised and classified for seedling characters. Ten days to two weeks after seeding, the plants can be classified for such characters as: green (*a*) and purple stem, yellow (*Xa*) and green cotyledons, dwarf (*d*) and tall, woolly (*Wo*) and normal. The plants can be sorted and transplanted or left in situ. The ratios obtained can be checked at weekly intervals by the same or other students. By the time the plants have been growing for six weeks it is possible to classify 16 different characters, although not all of them are compatible in the same cross. These seedling characters give examples of standard monohybrid and dihybrid ratios, as well as of 2:1 lethals (*Wo, Xa*), 6:2:3:1 (*Wo, a*), 9:3:4 (*H, hl or b, c*), 9:7 (*a, al*) and a linkage ratio with 20 percent cross-over (*a, hl*).

Pigment Genes

There are several genes which control the anthocyanin and plastid pigment systems. The mode of action of these genes is worth investigating by the methods of physiology and biochemistry, especially since gene dosages from none to four can easily be obtained in tetraploids. The anthocyanins are controlled chiefly by the alleles *A/a* for green and purple stem, and *Al/al* for purple stem which turns green two weeks after germination. The *al al* plants vary in the time of loss, and in the completeness of the disappearance of the purple pigment. The double recessive (*a a al al*) is green, but the autonomy of the two genes in graft hybrids has not been tested.

The genes lutescent and xanthophylous both produce yellow plants but differ in their action. Lutescent has a green growing tip, and the leaves gradually turn yellow. The speed of the change from green to yellow is greatly retarded when the soil is high in nitrates. Plants with the xanthophylous gene are yellow when they emerge from the soil, and stay yellow throughout their life, the

*I should like to acknowledge my indebtedness to the University for providing research grants, and to The Department of Horticulture, Ontario Agricultural College, for growing the experimental plants. Also to Miss E. Cormack for drawing the chart of the linkage groups.

color not being affected by the nitrate content of the soil. There is also an unnamed gene which causes the plant to be yellow-green instead of green, this character is found in the variety Golden Colossus. The two genes for uniform unripe fruit also affect this pigment system but they are localized in their action, apparently affecting only the stem end of the fruit. The two genes are distinct genetically, but except under certain light conditions, they have identical phenotypes.

The lycopene and carotene pigments of the fruit are controlled by at least two sets of alleles: the red/yellow, and the tangerine orange/non-orange. These two pairs of alleles give four colors: red (*R-T-*), yellow (*rrT-*), dark tangerine orange (*R-tt*), and light orange (*rrtt*). These four colors can be increased to eight by the addition of the alleles *Y/y*. The action of these genes is confined to the fruit epidermis; *Y* produces a yellow pigmented cell, and *yy* leaves the cells non-pigmented, so that the fruit has a clear skin. A red fruit with a clear skin is pink instead of red.

Fruit Abscission Gene

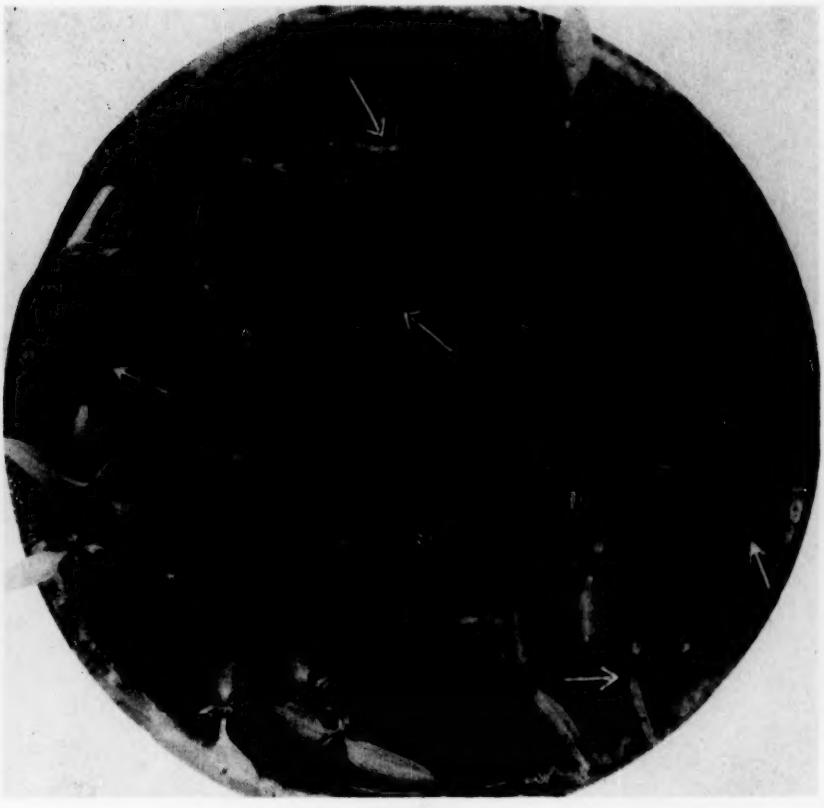
Most tomato varieties have an abscission joint in the pedicel, so that when the fruit is picked, the calyx and part of the pedicel remain attached to the fruit. The position of this joint, and the laying down of the corky cells which make it function, is a good research project in developmental genetics. The gene *j* completely suppresses this joint, and in such plants the calyx remains attached to the plant instead of coming off with the fruit. Sometimes corky cells are laid down between the calyx and the epidermis of the fruit. In many genotypes, the *mc* gene also makes the pedicel appear jointless, but close inspection shows that an ill-defined joint does exist, although no corky layer develops. The gene *bu* also affects this abscission layer which is normally situated on the pedicel about half-way between the calyx and the peduncle. In bushy (*bu*) plants, the joint is moved in a distal direction to a point close to, or touching the calyx.

Fruit Shape Genes

Fruit shape presents another developmental problem which has never been solved. The ordinary somewhat spherical fruits of commercial tomatoes contain the major fruit shape gene *O*, whereas the varieties Yellow Pear, and Yellow Plum have the recessive gene *o*. Normally, in a cross where one of the parents is pear-shaped, the F_2 segregates are also pear-shaped, although the neck of some fruits may not be as constricted as in the parent. When the parent is plum-shaped, the majority of the segregates are also plum-shaped, but a few are pear-shaped. Crosses between plum and pear-shaped parents show that both are manifestations of the same gene locus, but they have not been studied in enough detail to reveal whether the differences in shape are the result of multiple alleles or of modifiers. Besides this major gene, there is at least one other pair of alleles and possibly two. The elongation of fruits in the varieties Beefheart and Oxheart is the result of a different set of genes, which in the few crosses studied gave a 3:1 ratio with no linkage to dwarf. The segregate classes are not as distinct as in F_2's segregating for round and pear. The variety San Marzano has an elongation gene, which on limited evidence appears to be distinct from either of the other two sets of alleles. There are probably other genes which also control the elongation of fruit. Crosses involving the two or three sets of alleles mentioned, and the fasciated and locule number genes, which broaden fruit, would make an interesting and profitable study of gene action.

List of Gene Symbols and a Description of the Characters

The alphabetical list of characters given below is not a complete list of all characters which have been described, but includes only the ones which are in the seed stocks of this laboratory, and have been tested for monogenic segregation. Several other genes have been provisionally named, but the stock has either been lost or else the material is not suitable for linkage studies. As examples of named genes which at present are unsuitable for linkage work, can be listed the male sterile genes of Rick[11] (ms_1, ms_2 or ms_5) which show monogenic segregation as long as they are in the presence of San Marzano genotype, but when they are outcrossed to "test" parents, there are no segregants that can be classified as male sterile. In such situations there are problems of either penetrance or modifiers to be solved before linkage can be tested by the use of the standard stocks. The beta-carotene gene of Lincoln and Porter[7] is postulated on the basis of a trimodal curve in the F_2. No F_3 plants were grown to prove the interpretation or to show the amount of overlap. The lack of discrete segregate classes in the F_2 makes linkage studies difficult and unreliable.



NARROW COTYLEDON—A NEW CHARACTER

Figure4

A few of the twelve narrow cotyledon (*ncnc*) F_2 segregates in this photograph are marked by arrows. Fifteen of the 41 *Nc* segregates, were removed before the photograph was made.

**a*—ANTHOCYANINLESS or green stem. Homozygous *aa* plants do not develop purple pigment in any part of the plant. In *A*– plants, the amount of pigmentation varies inversely with the rate of growth of the plant, and classification is best made when the plants are not growing too actively.

**al*—ANTHOCYANIN-LOSER. In *alal* plants, the stem is purple when the seedling emerges from the soil. Ten days to three weeks later, the purple color disappears leaving dark purple islands surrounded by green tissue. Within three days after this process begins, the stem is entirely green except for the base of the hypocotyl which sometimes remains purple.

**b*—BROAD LEAF. Leaves of *bb* plants are wider than the normal leaf, and is

*Genes marked with an asterisk have high expressivity and are easily identified. They are recommended for use as class material.

THREE TYPES OF HAIRY STEM

Figure 5

A—Hairless (*hlhl*) is epistatic to other genes conditioning stem and hair length. No hairs are present, but glandular trichromes are abundant. *B*—Smooth plants (*HH*) lack hair except at the base of the stem and on the growing tip. *C*—Plants homozygous for the hairy allele (*hh*) have hair present on all parts of the stem.

more entire with a few sharp-pointed basal lobes. This gene came from Sandsome as Jorgenson's "potato leaf." (Illustrated in *Journal of Heredity* 42: 101, 1951.)

bk—BEAKED FRUIT. Plants with the genotype *bk bk*, have a pointed beak-like process, 5-10 m.m. long at the stylar end of the fruit. The beak is best developed in pear-shaped fruits with two locules.

br—BRACHYTIC. Brachytic plants have shorter internodes than normal ones. At six weeks of age, the brachytic plants are only about one-half as tall as the *Br* segregates; they also have a more spreading growth habit. This character came from the variety, Rouge Naine Hative.

bu—BUSHY. Plants homozygous for *bu* are similar to brachytic, but more spreading, with the leaflets placed further apart on the petiole. The plants are surculose, which accounts for the bushy appearance of older plants. Bushy was one of MacArthur's X-ray mutations.

**c*—POTATO-LEAF. A variant characterized by almost entire leaflets which lack the dentations of the ordinary cut-leaf varieties. The varieties Red Jacket and *L.e. var grandifolium* have potato leaves. (Illustrated in *Journal of Heredity* 42, page 101, 1951.)

Cf$_{P1}$—CLADOSPORIUM RESISTANCE—P_1. The dominant allele gives immunity to leaf mold caused by physiological races 1, 2, 3 and 4 of *Cladosporium fulvum*. This and the next two characters are fully described by Langford.

Cf$_{P2}$—CLADOSPORIUM RESISTANCE—P_2. the dominant allele gives resistance to physiological races 1, 2, 3 and 4 of *C. fulvum*, and along with *Cf*$_{P1}$, was isolated from *L. pimpinellifolium*.

Cf$_{sc}$—CLADOSPORIUM RESISTANCE—*sc*. This dominant allele of the gene, derived from the Sterling Castle variety, gives resistance to races 1 and 3 of *C. fulvum*.

**d*—DWARF PLANT. Homozygous *dd* plants have shorter hypocotyls and broader cotyledons, the stems are shorter and thicker, and the leaflets more sessile and rugose. The variety Dwarf Aristocrat has the *d* gene.

**dl*—DIALYTIC PLANTS. Flowers of *dl dl* plants are characterized by stamens which are not united into a tube. The distal end of the stamens are usually spread apart and the application of slight pressure will cause the stamens to spread completely. This gene came from Rick[10], and was first discovered in the San Marzano variety.

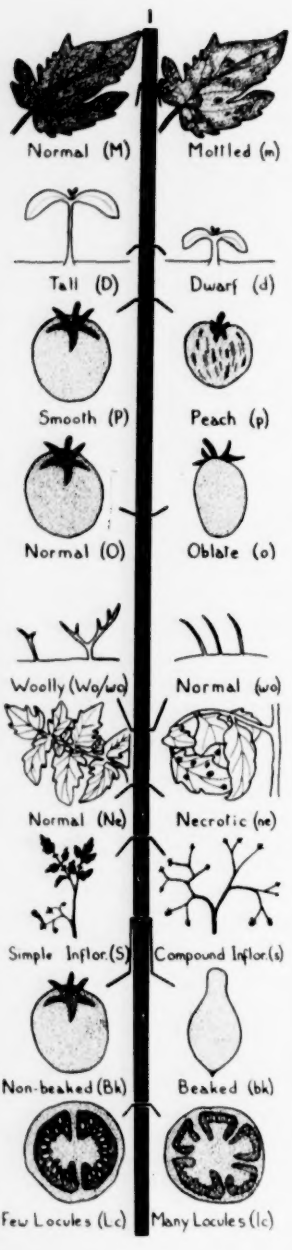
dm—DWARF MODIFIER. This condition occurs in the variety Burbank Preserving. In dwarf plants (*dd*), the *dm* allele produces an extreme type of dwarf with a more upright type of growth. In tall plants, the *dm* allele has no observable effect.

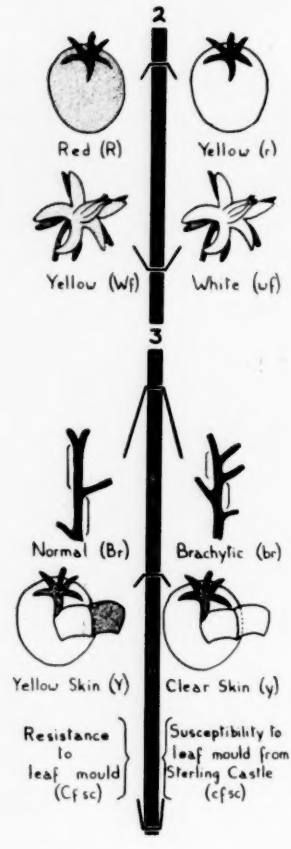
e—ELONGATION OF THE FRUIT. This character is shown in the varieties Beefheart and Oxheart. It segregates as a recessive in certain crosses. The genotype *FFee* is usually plum-shaped while *ffee* fruits are heart-shaped.

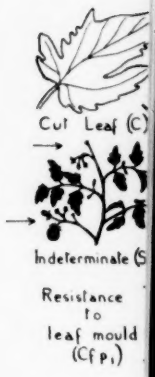
f—FASCIATED. This recessive gene when homozygous increases the locule number, produces a dorsal/ventral flattening of fruit, and a rough or lobulated outline. The degree of lobulation is affected by modifiers, so that *F/f* segregation is not clear-cut in certain crosses.

**fl*—FLESHY CALYX. Plants exhibiting this variation have thickened fleshy sepals, especially on the ripe fruit. (This charter was obtained from P. A. Young and W. A. Frazier.)

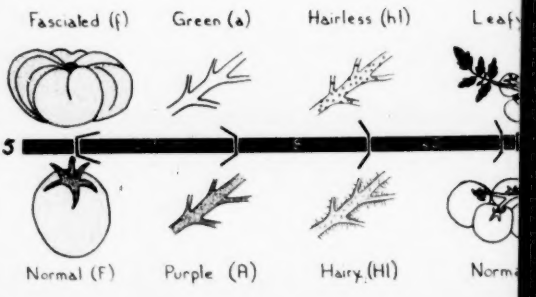
**H*—HAIRY STEMS. Commercial varieties with hairy stems are due to this recessive gene (*hh*), whereas the varieties Burbank Preserving, and Red Currant (*L. pimpinellifolium*), have smooth stems with the genotype *HH*. The F_1 of the cross smooth $\times$ hairy, is slightly hairy at the growing tip, but the hairs disappear as the stem becomes mature. With careful observation, it is possible to classify the F_2 into smooth, slightly hairy, and hairy, in a 1:2:1 ratio. In smooth plants, the hypocotyl is hairy. (Figure 5*C*). The relative

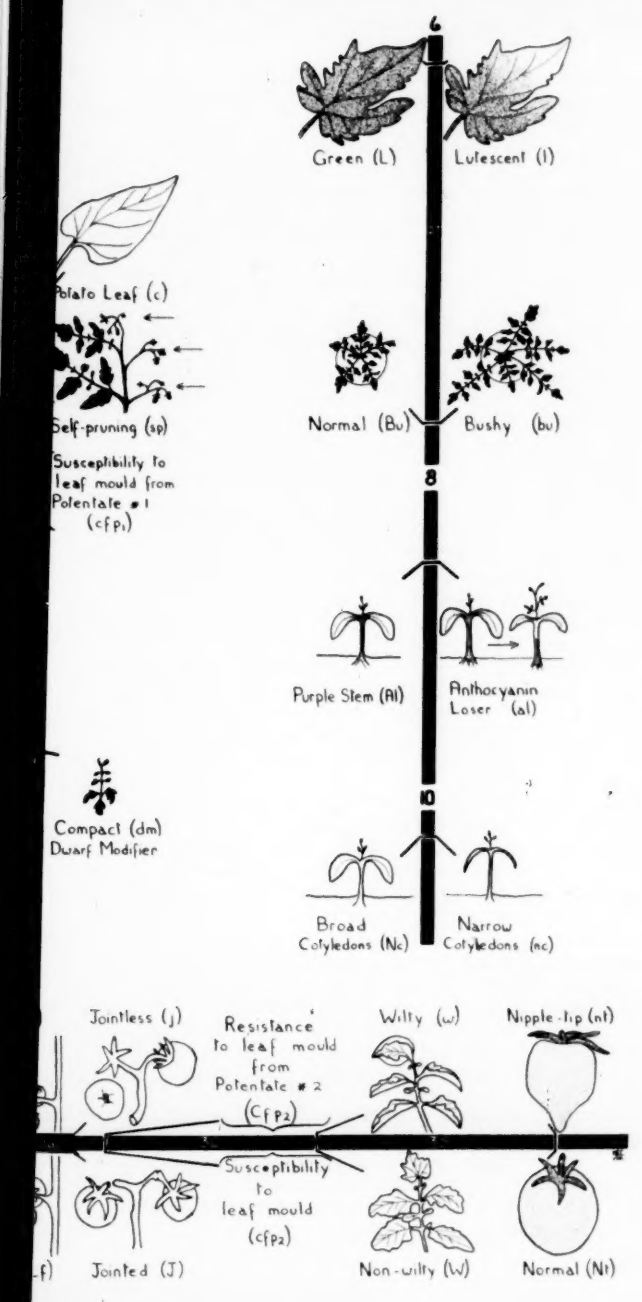

1
Normal (M)
Mottled (m)
Tall (D)
Dwarf (d)
Smooth (P)
Peach (p)
Normal (O)
Oblate (o)
Woolly (Wo/wo)
Normal (wo)
Normal (Ne)
Necrotic (ne)
Simple Inflor.(S)
Compound Inflor.(s)
Non-beaked (Bk)
Beaked (bk)
Few Locules (Lc)
Many Locules (lc)


2
Red (R)
Yellow (r)
Yellow (Wf)
White (uf)
3
Normal (Br)
Brachytic (br)
Yellow Skin (Y)
Clear Skin (y)
Resistance to leaf mould (Cf sc)
Susceptibility to leaf mould from Sterling Castle (cf sc)


Cut Leaf (C)
Indeterminate (S
Resistance to leaf mould (Cf p1)

Spread (Dn
Dwarf


Fasciated (f)
Green (a)
Hairless (hl)
Leafy
5
Normal (F)
Purple (A)
Hairy (Hl)
Norma



A LINKAGE MAP OF THE TOMATO

Figure 6

At the present time, seven linked systems of genes have been identified in the tomato, and five other genes—not established as being linked with each other—or with any of the linkage groups, have been designated as markers for the remaining linkage groups. The other genes in the accompanying list are still in process of being tested

density of long, short, and glandular trichomes on the hairy plants varies greatly and appears to be polygenic in inheritance.

**hl*—HAIRLESS. Plants homozygous for *hl* are characterized by the complete absence of trichomes except for some glands filled with watery fluid, which often give a white speckled appearence. The plant is weak and breaks easily, and the stamens because of the lack of hair, tend to be dialytic. The seed was obtained from E. A. Kerr of the Horticultural Experimental Station, Vineland, where hairless arose as a mutation. Hairless can be distinguished from smooth (*HH*) by the absence of hairs on the hypocotyl (Figure 5*A*, *C*). Hairless × smooth gives an F_2 ratio of 9 smooth : 4 hairless : 3 hairy.

**j*—JOINTLESS. Flower pedicles of jointless plants lack the abscission layer found on the dominant commercial types. When the fruit is picked, the break occurs at this layer so that in the jointed kind, the calyx and part of the pedicel remain attached to the fruit, whereas in the jointless kind, the entire fruit comes off leaving the calyx on the plant. (Illustrated in Butler[2].) Its relationship to leafy inflorescence *lf* has not been fully determined. It appears to be a close linkage, with *Lfj* pollen only partly viable.

**l*—LUTESCENT OR YELLOW. Plants displaying this recessive phenotype have growing points and new leaves which are normal green. They gradually turn yellow with advancing age.

lc—FEW LOCULES. Most pear-shaped fruits have only two locules. Such plants possess the recessive gene *lc* which restricts the number of locules. This is not the only hereditary control over locule number, which is also influenced by the alleles *F*/*f* and by polygenes.

lf—LEAFY INFLORESCENCE. Most commercial varieties of tomatoes do not have any leaves on the inflorescence, but the variety Rouge Naine Hative has leaves on all inflorescences, and this character behaves as a simple recessive. In certain crosses, the leafy segregates instead of having a simple leaf growing from the inflorescence, have running flower trusses.

**m*—MOTTLED LEAVES. One of MacArthur's X-ray mutants has cotyledons and leaves which are mottled with light-yellowish-green. Superficially this looks like mosaic and breeds as a simple recessive.

**mc*—MACROCALYX. Plants homozygous for *mc* have sepals which are leaf-like and are enlarged up to six times their normal size. (Illustrated in Young and MacArthur[15], page 30.)

nc—NARROW COTYLEDON. This character arose from an X-ray mutation of MacArthur's. It is characterized by cotyledons which are only half as wide as normal. Such seedlings usually grow more slowly than normal ones. See Figure 4.

nc—NECROTIC. Plants show a progressive breaking down and death of the tissue without the presence of any pathogens as described by Langford[5]. The *Nc* allele came from *L. pimpinellifolium* and conditions the compatibility of this species with *L. esculentum*.

**o*—OBLATE OR PEAR-SHAPED. Fruits showing this form segregate as a simple recessive. Many plum-shaped fruits are the result of the same gene.

**p*—PUBESCENT OR PEACH FRUITS. This character is shown by hairs on the skin of the fruit, and leaves covered with a greyish-blue bloom.

**pc*—STICKY PEEL. Tomatoes displaying this quality have a fruit epidermis which is peculiarly cutinized and almost hairless, so that it feels sticky to the touch. Most segregates have bundles of long red crystals in the epidermal cells and have a different flavor. Plants with sticky-peel have lighter green leaves and very hairy stems. The monogenic nature of these hairy stems has not been established. Preliminary analyses indicate that the lighter-green of the

foliage is due to a linked gene which is four to ten units away from the gene for sticky peel. This mutant appeared in the Prairiana variety, Young[14].

*y—YELLOW FRUIT. This color is allelic with the dominant red fruit color. *R-Y-* fruits are red, *R-yy* fruits are pink, *rrY-* fruits are yellow and *rryy* fruits are white (very light yellow).

*s—COMPOUND INFLORESCENCE. The recessive allele conditioning this variation is allelic to the simple inflorescence found in standard varieties. In compound inflorescence, the pedicle becomes much branched, so that there are often as many as 80 flowers on a single inflorescence. This type of inflorescence came from the variety Grape Cluster.

*sp—SELF-PRUNING OR DETERMINATE GROWTH. There are two types of self-pruning plants, caused by the same gene. It is not known whether these differences are the result of multiple alleles or modifiers. In one type, the plant produces the inflorescence at the growing tip, and new growth has to come from axillary buds. Sometimes this new growth consists entirely of flower trusses and no leaves, and at other times, one or two leaves occur between trusses. (See Young and MacArthur[15], page 16). In the other type, stem growth is normal but the flower trusses grow from each node instead of every third node (see MacArthur[8]).

*t—TANGERINE ORANGE FRUIT COLOR. In the presence of the *R* gene for red the (*tt*) fruits are a rich orange, and when the genotype is *rrtt* the color is light orange. The skin color gene *Y* also changes the external fruit color so that the three sets of alleles *Rr*, *Tt*, and *Yy* give eight different colors of fruit. The tangerine gene also produces an orange staminal cone instead of the normal yellow one.

*u—UNIFORM FRUIT. Plants of the genotype *uu* produce fruit which lack the dark green cap found on the stem end of non-uniform (*U*) fruits. This darker-colored cap is usually later in ripening than the rest of the fruit, so that fruits lacking this cap are also called uniform ripening. The lack of this cap with its more persistent green often results in uniform green fruits being picked at an earlier degree of ripeness than non-uniform fruits.

ug—UNIFORM GREEN. Fruit displaying this character is almost identical phenotypically with uniform fruit. It is usually apple-green in color as opposed to the yellow-green of the uniform fruits. Shading and exposure to the sun affect these colors so that it is often impossible to separate *u* from *ug* plants by their phenotype. (See Bohn and Scott[1]).

va—VASE-SHAPED FLOWERS. An example of this character found in the functional male sterile John Baer variety (Rover[12]) gives a good monohybrid segregation. Although these flowers produce abundant good pollen, they rarely self and are therefore sterile. The petals stay attached to the staminal cone with only the tips of the corolla spreading.

w—WIRY. Plants homozygous for wiry are dwarfed, with slender wiry or strap-like leaves. The plant looks as though it is suffering from shoestring mosaic. Flowers are produced on wiry plants, but only rarely can they be coaxed to produce fruit and seeds. (See Lesley and Lesley[6]).

wf—WHITE OR TAN FLOWER. The yellow corolla of the normal tomato flower is replaced by a tan or white color corolla. (See Young[13]).

*wo—WOOLLY. The trichomes of woolly plants are no longer than in the normal type, but they are branched and often stellate. They appear on the fruit as well as the other parts of the plant, but unlike the peach pubescence of the gene *p*, they are easily rubbed off. The plants have grey leaves and stems. The original came from W. S. Porte who called it angora. When selfed, woolly gives a ratio of two woolly to one normal, with a few plants

which lack a plumule and soon die. It is assumed that *WoWo* genotype is lethal, and these defective plants may represent a small portion of the *WoWo* plants. Woolly is epistatic to *H* or smooth, both *WoWo H H* and *Wowo hh* plants are woolly, but the *Wowo H H* plants lack the long hairs.

wt—WILTY LEAVES. The leaf margins are rolled up as though the plant is suffering from a moisture deficiency. The expression of this character varies greatly in different crosses. Some crosses are always deficient in wilty segregates, less than one quarter of the plants being wilty, whereas in other crosses, the segregates divide into one non-wilty, two slightly wilty, to one extremely wilty. Soil and growth conditions also affect the expression of this gene. Wilty came originally from the variety Rouge Naine Hative, which is extremely wilty, and all linkage work was done with the gene from this source. Some of the American varieties are slightly wilty, and fragmentary evidence indicates that this is due to a mutation at another locus.

*Xa—XANTHOPHYLLIC LEAVES. This yellow-leaved variant is dominant to normal green leaf (*xa xa.*) The mutant first occurred as a chimera in the tomato field at Guelph in 1936. Seeds from the green shoots of this plant gave nothing but green, while seeds from the variagated branches gave a mixture of yellow and green seedlings. Seeds produced on the yellow branches gave two yellows to one green (528:274). There were also 32 plants which were a brighter yellow, with shorter hypocotyl, narrower cotyledons, and which died in the first two weeks. It is not known whether these represent some of the *XaXa* lethals or some of the *Xaxa* plants which have been more adversely affected than others.

*y—CLEAR FRUIT SKIN. The yellow pigment is not present in the epidermal cells of the fruits as is the case in the dominant yellow-skinned *Y* plants. The character is easily seen by stripping back the epidermis and holding it up to the light. The genotype *RRYY* is red, *RRyy* is pink *rrYY* is yellow, and *rryy* is white.

The Linkage groups

The 12 linkage groups consist of two groups with eight genes, one group with four, two groups with three, two groups with two and five groups each with a single marker gene. Most of the linkage data have been published in Butler[2] and MacArthur[9]. The data accumulated since these publications have been utilized in calculating the crossover units given on the chart, so that these may differ slightly from previous values. The crossover values are given as whole units and no attempt is made to indicate their relative accuracy except in generalized statements given below.

In *group 1*, the order and distances for the genes *m d p o s bk* is well established. Woolly and necrosis are both between *o* and *s*, but their order is not too well established. Woolly, because of its lethel effect, and necrosis because it only appears in the species hybrids, are both harder to work with than the other genes. The data on *lc* are less extensive than that for the other genes.

Group 2 is a relatively new linkage, 2541 plants in F_2's and back crosses gave a combined crossover value of 14.9±2.2.

Groups 3, 4, 6, and *7* are based on extensive data, and it is not expected that any radical changes in order will be made in these groups.

Group 5 was rewritten last year, (Butler[2],) to include the genes *wt* and *nt* from group 10. The new mutant *hairless* (*hl*) is found to be in this group, the linkage data are given below.

F_2 repulsion.
Hl A 630: *Hl a* 279: *hl a* 263: *hl a* 8
χ^2 *Hl/hl* 3.03
χ^2 *A/a* 0.38 Cross-over 17.7 ± 2.9%
χ^2 linkage 29.87
Hl J 44: *Hl j* 22: *hl J* 21: *hl j* 1
χ^2 linkage 7.29 Cross-over 20.6 ± 10.1%

These data would indicate that hairless is between *a* and *j*, although the data for the second cross-over are too small to draw anything but a tentative conclusion. Extensive backcrosses are needed for this chromosome to fully substantiate the order of these genes, and to give more reliable recombination values. The loci *lf* and *j* continue to give unequal recombinant classes, the latest F_2 coupling ratio being *Lf J* 4601 : *Lf j* 96 : *lf J* 34 : *lf j* 1478. One jointless non-leafy selection was grown all summer and never produced a single leafy inflorescence, but cuttings from this plant did have leafy inflorescences. Another selection which was non-leafy and jointless, refused to self, but set fruit readily when other pollen was used. Until the material has been studied further, it is impossible to tell whether we are dealing with environmental or genetic modifiers of leafy, pollen sterility, or very close linkage.

The marker genes in *groups 8* to *12*, have been tested with all linkage groups and give a negative linkage with small standard errors in all cases. The negative linkages for *nc* in group *10* have not been published, but they are extensive enough to substantiate placing narrow cotyledon in this group. It is expected that some of the unplaced genes mentioned below will soon be placed, and the full data can be published at that time.

The unplaced genes have not been completely tested, but they show 50 percent recombination with groups mentioned. Dialytic is not in *groups 1, 3, 4, 5, 7, 8, 11* or *12*. Sticky peel is not in *groups 3, 4, 5, 11* or *12*. There is tentative evidence that it may be in *group 7*. Wiry is not in *groups 1, 4, 5, 6, 7* or *8*. The rest of the new genes are still in the preliminary stages of testing.

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TWINS AND POLIO

BECAUSE of the recent awareness that many more persons have a "benign" polio infection rather than the severe paralytic type, much attention has been given to the possibility that susceptibility to paralytic polio may be an inherited characteristic of the individual determined by a genetic factor.

The existence of such a genetic factor has been suspected by many investigators. Aycock and others have presented pedigrees of families with a high frequency of poliomyelitis among the members. Interesting also was the report of Addair and Snyder who found blood relationships in all 29 cases of polio occurring over a fifty year period in a remote district of West Virginia. From their findings they suggested the possible existence of a recessive gene as responsible for susceptibility to paralytic poliomyelitis.

It occurred to Drs. C. Nash Herndon and R. G. Jennings that additional, perhaps more critical, evidence regarding the genetic influence on susceptibility to poliomyelitis may be secured if the disease incidence were studied among twins. The case for genetic influence would be strengthened if one finds more instances of paralytic disease affecting both members of twins of monozygous type (i.e. identical twins) than among the dizygous type (unlike twins). It would indicate that

the trait in question—susceptibility to paralytic poliomyelitis—occurs with a greater frequency among individuals derived from a single ovum (and therefore sharing the same chromosomal pattern) than among those originating from two ova. This was the theoretical approach adopted by Drs. Herndon and Jennings in their twin family study of susceptibility to poliomyelitis. Their study is presented in the *American Journal of Human Genetics* for March 1951.

This series included a set of two-egg triplets, a boy and two girls, the latter derived from a single ovum. For purpose of compilation, the triplets were considered as two pairs of dizygous twins. There were then 47 twins compiled in the study. Of these, 14 were determined as identical (monozygous) and 33 as unlike (dizygous). Of the 14 monozygous group, *paralytic* poliomyelitis affecting both twins occurred in five pairs (the "concordance" rate thus being 35.7 per cent). Of the 33 dizygous group, paralytic involvement of both twin members occurred in only two instances (the concordance rate, 6.1 percent).

"It is thus demonstrated that both members of monozygous twin pairs present paralytic poliomyelitis more often than do dizygous pairs, and that this difference is statistically significant with a probability level of less than one percent."

The difference in incidence between monozygotic and dizygotic twins indicates the existence of a measurable genetic influence on susceptibility to paralytic poliomyelitis. The data are not sufficient to reach conclusions as to the number or kind of genes involved. Since none of the 87 parents of the twins examined had a history of poliomyelitis, the gene involved appears very unlikely to be a dominant gene. Nor is there sugggestion that sex-linked genes are involved.

If a recessive gene is implicated, then the susceptibility must be manifested by those individuals homozygous for this gene. And since paralytic poliomyelitis is not a rare disease, this recessive gene determining susceptibility must be one of a relatively high frequency in the total population and persons who carry this gene must be quite numerous. If a rare recessive gene were the one responsible, a significant portion of the parents of these cases should have been related to each other by blood (cousin marriages). "None of the parents are known to be related, and it is demonstrated by pedigree that any possible relationship is more distant than third cousins."

"Another possible interpretation of these findings is that susceptibility may be due to multiple gene effects. The data are insufficient for critical evaluation of this possibility."

That the inherited susceptibility is by no means *the decisive* factor in determining the reaction of individuals to exposure may be inferred from the fact that even among persons of identical genetic endowment (monozygous twins) in the same households, paralysis involving both members occurred in only 35.7 percent of the pairs.

National Foundation For Infantile Paralysis

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Mutating Concepts of the Gene

"... DURING the early development of genetics the gene was regarded as a material particle that could account for the transmission of hereditary traits. Then it became the particle in which mutation occurs. Finally it was thought to be the particle that plays a special role in the biochemistry of the cell. Thus it was being attacked from three different angles—by three different attackers. The same thing happens when three climbers approach the summit of a mountain from different sides; although it is the same mountain it may look very different to each climber.

"Two years from now the Ninth International Congress of Genetics will be held in Italy, and it is safe to make the prediction that many of these present ideas will then look obsolete. But, just as the rate of change in living things can be taken as a good measure of evolutionary progress, so can the rate of change of ideas be considered as a sign of the health and vitality of a science."

HARRIET EPHRUSSI TAYLOR

Scientific American, October, 1951

THE PIEBALD HAMSTER

A Mutation Showing Growth Retardation and Urino-Genital Abnormalities

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THE piebald hamster was first described by Foote[2] who suggested that this color variation might be a recessive factor, and stated that it is characterized by small body size and lowered resistance. This paper is to confirm his report and suggestions as to the genetic pattern, to present graphically the size differences during development, and to report another anomaly, aplasia of parts of the urino-genital tract, which may be associated with the piebald mutation.

In the spring of 1947 a dissimilarity of coat color was noted by the author within a single litter of young animals, soon after a group brought from Cornell[4] was merged with some used at Duke[1]. The color difference disappeared with maturity but the litter was selected for deliberate inbreeding, and by the following fall one adult piebald male was obtained. Deliberate inbreeding and backcrossing have been continued since that time in an attempt to establish the genetic pattern. In 1950 a new colony was established at Wisconsin from two piebald males and continued until June 1951, when all but one of the females were killed. The males were saved to propagate a new colony when so desired.

Inheritance

Although there is considerable variability in the degree of white spotting, due very likely to modifying factors, the basic piebald pattern appears to depend on a single recessive factor, as Foote[2] has suggested. Piebalds appear in stocks only after inbreeding, and when crossed with unrelated normal animals produce only normal offspring. Matings between two piebalds have resulted so far in 34 offspring. All but one of these were clearly piebald. This one was a doubtful piebald, having a light spot in the dorsal area. He was not examined until two weeks after birth, so it is not known whether he would have been definitely piebald if examined earlier.

Crosses between piebalds and normals of a piebald parent produce mixed litters, as would be expected with recessive inheritance. However, instead of the expected 1:1 ratio of normal to piebald, the 18 matings produced a total of 49 normal and 24 piebald offspring. This suggests that only about 50 percent of the piebald zygotes survive until the time of recording. This is supported by the data on litter sizes. Litters with piebalds averaged 4.2, those with a 1:1 expectation averaged 5.1, and normal litters about 7.0†. There is no evidence of sex-linked inheritance, and the viability effects seem to act on both sexes approximately equally. Out of 69 piebald individuals classified as to sex, 35 were female and 34 male.

Urino-genital Aplasia

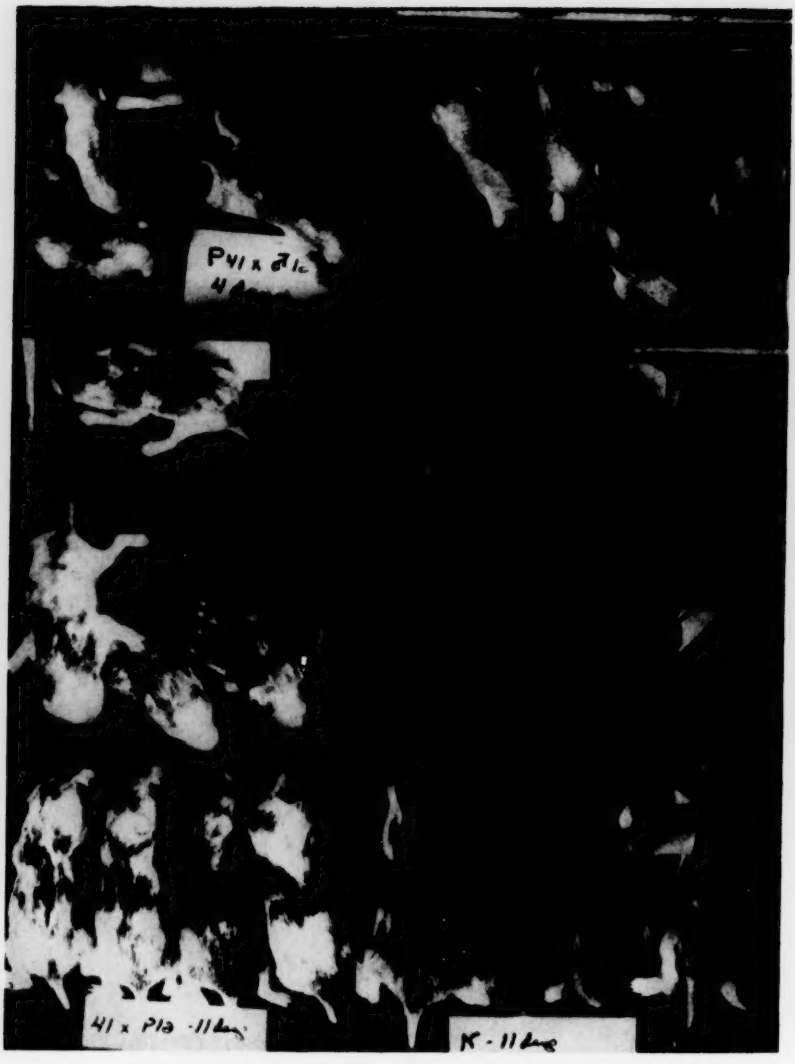
In addition to its effect on viability, the

TABLE I.—Urino-genital abnormalities and breeding behavior. The last three animals, indicated by N, were normal colored. Symbols are as follows: x-aplasia, c-cystic, s-small, am-amorphous mass, a-aborted, l-normal litter, st-apparently sterile, n-not mated.

	Kidney and ureter		Uterus					
Animal Number	Right	Left	Right upper	Right lower	Left upper	Left lower	Vaginal orifice	Breeding record
105		x				x		a
103	x			x	x	x	x	s
113		s	x	x	c	x	x	s
106		x			c	x		l
E2		am	x	x	x	x	x	s
120		x			c	x		a
41			x	x				l
44			c	x	c	x	x	s
45	x		c	x	c	x	x	s
54			c	x	c	x		s
67			c	x				n
N-1			x	x				l
N-2	c							s
N-3		x			x	x		s

*Post-doctoral Fellow of the National Cancer Institute, National Institute of Health, Public Health Service, Federal Security Agency. The author is indebted to Dr. James F. Crow, Departments of Zoology and Genetics, University of Wisconsin, for the genetic analysis.

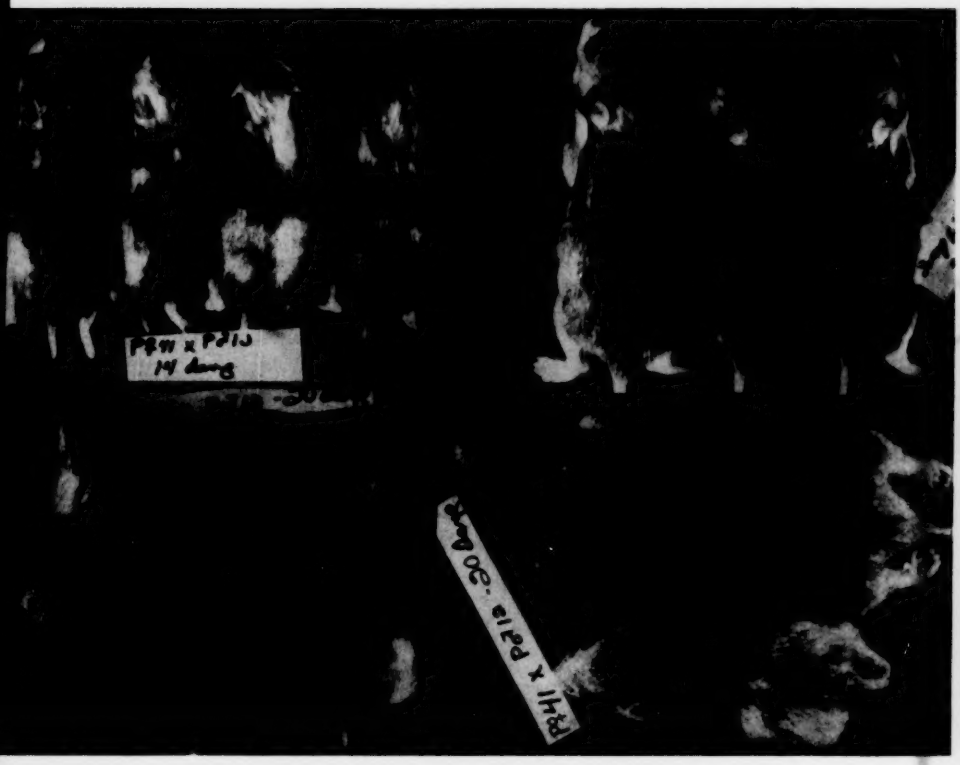
†A recent paper by Foote and Foote[3], not seen until after this manuscript was prepared includes data on litter size that are in substantial agreement with those given here.



NORMAL AND PIEBALD HAMSTERS AT VARIOUS AGES

Figure 7

These photographs show two litters born the same day. Photographs were made with the same magnification and lighting conditions. *A-B*—Piebald litter and normal litter at four days post partum. *C-D*—Piebald and normal at seven days; *E-F*—piebald and normal at 11 days. At this stage, the normal have considerably outgrown the piebalds.



COMPARISONS AT TWO AND THREE WEEKS

Figure 8

A-B—Normal and piebalds at 14 days. *C*—Piebalds at 20 days. *D* shows one of the piebald litter compared with one of the normal litter to show the extreme difference in size at 20 days post partum.

piebald factor is associated with aplasia of the urino-genital tract in the females. The degree of aplasia appears to be to some extent correlated with the degree of piebaldness and is also highly variable, ranging from complete absence of the uterus and a kidney and a non-patent vagina to failure of development of part of one uterine horn. Of 41 piebald females autopsied, 11 showed aplasia. The extent of abnormalities in these 11, as well as the breeding history, is shown in Table I. In none of these was the ovary or oviduct affected. No aplasia was ever found in any of the normal colored litter mates of piebald animals.

In the course of some 1,000 autopsies three cases of aplasia of the female urino-genital tract (the degree and extent are indicated in Table I) were found in three normal colored individuals from three different commercial stocks. These were completely unrelated save for the common origin of all *Cricetus auratus* stocks from one original litter in 1930. It is not felt that these three should be regarded as bearing significance comparable to that of the piebalds, especially since other workers do not report finding such anomalies; the only confirmation is by personal letter from C. L. and F. M. Foote who report a high amount of aplasia among their piebalds.

Since approximately 25 percent of the piebald females autopsied have shown some ab-

normality whereas the frequency in normal animals is considerably less than one percent, the piebald condition must be somehow associated with these abnormalities, probably by pleiotropic action of the piebald factor.

The piebald males are apparently normal. One male, among about 50 studied, was cryptorchid until the age of five months. He proved to be sterile, and on autopsy lacked any seminal vesicles. Such an individual might, of course, have been found in any stock. Hence this isolated case does not justify any assumptoon that males are affected pleiotropically by the piebald gene as are the females.

Development of the Piebalds

The piebald pattern is clearly apparent by the time the first hair appears, as early as four to five days after birth. By seven days post partum the normal hamsters have a dark, almost black coat; the piebalds are pink with dark spots. From eight to 11 days of age the normal dark coat lightens to brown, while the piebald may deepen in color, even to the point of becoming obscured. In the adult the degree of piebaldness varies extremely from forms which are almost normal, save for unusual amounts of white about the face, to those in which the body is predominantly white with reddish brown spotting on the dorsal side.

The piebald, as Foote reports, is smaller than the normal. By 11 days post partum this is obvious to the naked eye, becoming more obvious throughout the next month of life. By 14 days post partum the body weights within one piebald litter varied from seven to ten grams, averaging 8.25 (It is interesting to note that the heavier animals are usually the darker. The paler the piebald, the smaller the individual). A normal litter, born the same day and reared under identical conditions, varied in weight from 10.75 to 14.50 grams, the average being 12.95. At 21 days the piebald litter varied from 17.75 to 22 grams, an average of 20.5. The normal litter varied from 34 to 44 grams, the average being 37. At 31 days another normal litter weighed an average of 57.32, a piebald litter of 42 days of age averaged 52.5. Moreover, normal members of mixed litters soon surpass their piebald littermates in size and weight. This suggests that the weight differences are genetic rather than being due to a nutritional factor of nourishment from the mother. With later development, this extreme size variation gradually diminishes.

Summary

The piebald pattern appears to be inherited as a single recessive, but with variable expression ranging from virtually normal to individuals with more than half the body surface white. There is about 50 percent reduction in embryonic viability, reduced size, and a significant fraction of the females have some urino-genital abnormality. Piebaldness is detectable with the first appearance of the hair, and affects the growth within 11 days.

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AN INTERSPECIFIC HYBRID IN BUDDLEJA

RAYMOND J. MOORE*

BUDDLEJA is a cosmopolitan genus of approximately 150 species of shrubs and small trees, widely distributed in the tropics and milder temperate regions. Several species are of ornamental value; three are rather commonly grown in Europe and in North America for their attractive spikes of small flowers. Previous hybridization work in the genus has been reviewed and described by Moore[4]; in all, at least ten artificial interspecific hybrids have been reported. An additional hybrid, *Buddleja asiatica* Lour. × *B. japonica* Hemsley, has now been produced.

Specimens of this hybrid have been deposited in the herbarium of the Division of Botany and Plant Pathology, Science Service, Dominion Department of Agriculture, Ottawa, Canada, and duplicates have been sent to the Bailey Hortorium, Cornell University, Ithaca, N. Y.

Fifteen flowers of an unusually late-flowering spike of *B. asiatica* were pollinated on July 7, 1948, with pollen of *B. japonica*. *B. asiatica* normally flowers in the greenhouse from November to January. A potted plant which was in bud in March was set outdoors and the development of the flower buds was delayed several months by the cold. Fourteen capsules containing a high percentage of apparently normal seed were picked on August 23. Some seed was sown immediately, more in the following January, and in both cases a high percentage germinated readily. The seedlings were slow-growing and delicate and many were lost through "damping off." About 12 seedlings were raised in the greenhouse and set outdoors in pots or planted in plots from June to September, 1949. Two plants were left outdoors over the winter of 1949-50; they did not survive. The remaining plants were grown under glass in the winter and again put out in the summer. During the two summers, the plants reached a height of about three feet and were full and bushy, but failed to bloom. In late September, 1950, one bush produced its first bloom and during the following January-April four seedlings flowered prolifically in the greenhouse. Except for a slight variation in flower color and in length of the panicle all of the plants are identical in appearance.

Description of the Parents

Buddleja asiatica Lour. (Figure 10*A*) is a woody shrub up to 15 feet in height, native to southeast Asia and the East Indies.

The leaves are opposite, 10-20 cm. by 2-3 cm., oblong-lanceolate, apex acute, base tapering, margin irregularly serrulate, almost entire, dark green and glabrous above, lighter and tomentose below. The flowers are borne in three-five flowered cymes arranged in a a slender pendulous panicle 10-30 cm. long. The corolla is white, glabrous without, yellow pubescent within; campanulate, five-six mm. long. The calyx is campanulate two-three mm. long, lobes one mm., triangular, acute, tomentulose. The stamen insertion is median; the ovary is ovoid, glabrous. The plant used as female parent is always self-sterile, as are all others of the species which the author has seen. The flowers have a very attractive sweet odor. This species blooms profusely from December to February and is commonly used by florists. *B. asiatica* is very tender: it will not survive winters at Ottawa, Canada (Zone III[5]), nor even in northern Virginia (Zone VI).

B. japonica Hemsley (Figure 10*B*) is native to Japan. Under favorable conditions it forms a full spreading bush up to six feet in height. The stems are square and winged. The leaves are ovate or oblong-ovate, 10-20 cm. long by three-five cm. broad, apex acuminate, margin irregularly denticulate, glabrous above, lighter, more or less glabrous beneath. The flowers are arranged in fascicles usually of three

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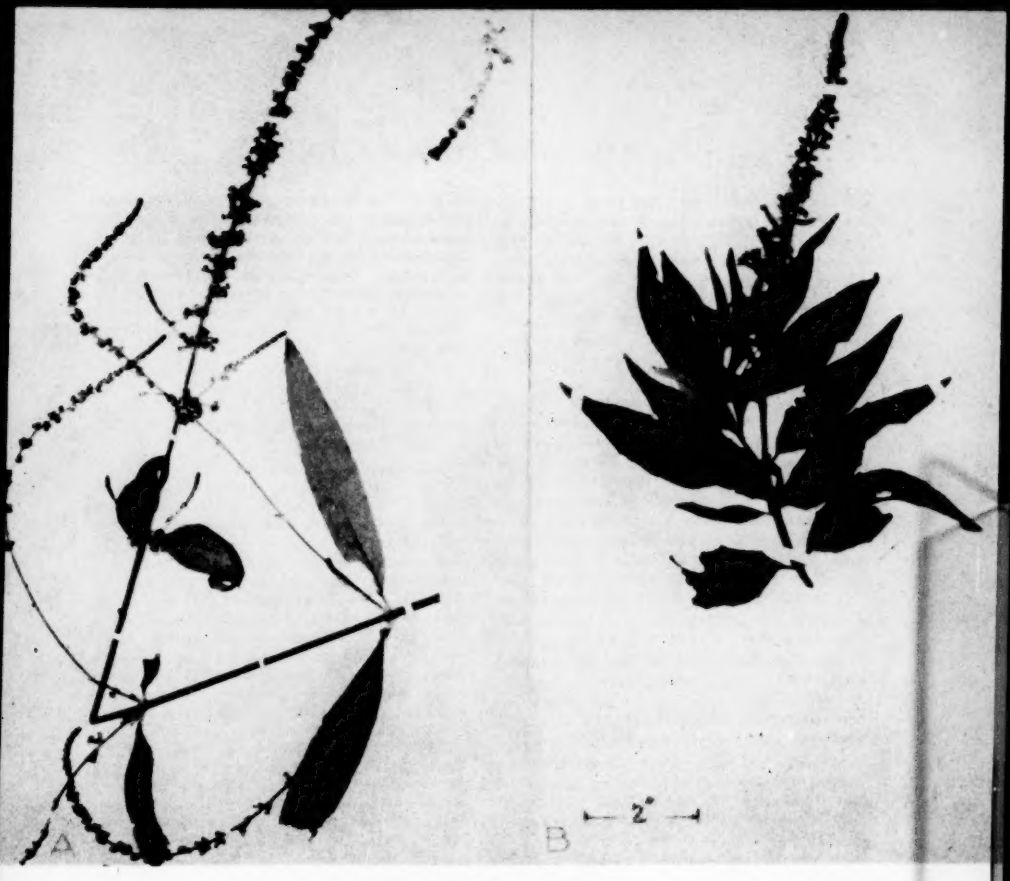
HYBRID *BUDDLEJA*

Figure 9

The F_1 hybrid of *B. asiatica* × *B. japonica* made by the author shows hybrid vigor in pannicle length and floret number, but the flowers are intermediate in size between those of the parents. Compare with parent species in Figure 10.



PARENT *BUDDLEJA* SPECIES

Figure 10

Buddleja asiatica is shown at *A*; *B. japonica* Hemsley at *B*.

flowers, these in turn form a compact pendulous panicle 10-20 cm. long. The corolla is curved, 15 mm., pale lilac gray-tomentose without, the four lobes darker lilac, two-three mm. long. The calyx is about four mm. long, lobes lanceolate, tomentose. The stamens are inserted in the lower third of the tube; the ovary is glabrous. All plants of this species which the author has seen, set seed heavily after self-pollination.

The flowers of *B. japonica* are not fragrant and the plant is one of the less ornamental species. At Ottawa, *B. japonica* blooms freely throughout July. The roots usually survive the winters although the tops are always killed here (Zone III).

Characteristics of the Hybrid

***Buddleja asiatica* Lour. × *B. japonica* Hemsley**

The first generation hybrid (Figure 9), forms a shrub about three feet tall and approximately the same in diameter under the conditions in which it has been grown at Ottawa. No doubt it would form a larger shrub in warmer climates.

The leaves are opposite, oblong-ovate or oblong-lanceolate, 10-20 cm. long by three-six cm. broad; dark green, glabrous or lightly pubescent above, lighter and pubescent below; apex acuminate, base cuneate, margin irregularly and slightly denticulate, almost entire, petioles five-ten mm. The stem is more or less square but is not winged. The flowers are usually borne in three-flowered cymes, arranged in a graceful terminal pendulous panicle 15-45 cm. long, 2.5 cm. broad tapering gradually to the tip. Several panicles may arise from the terminal portion of one branch, forming a graceful cluster of long spikes. The corolla tube is straight, 11 mm. long, 1.5 mm. broad, pale lavender, almost white, tomentose

without; four lobed, the lobes three mm. long, mauve 633/1-2 or cobalt violet 634/1-2 in color[1]. The throat of the corolla is pale yellow and is filled with long straight hairs. The calyx is six mm. long, green, tomentose, lobes 2.5-3 mm. long, triangular, acute. The stamens are inserted at a point immediately below the middle of the tube, about six mm. from the mouth. The ovary is conical, glabrous.

In Table I the hybrid is compared with the parent species with regard to the more striking characters in which the latter differ. In general appearance of foliage the non-flowering hybrid is very like *B. japonica*. However, the influence of the female parent appears in the intermediate size and color of the corolla. The inflorescence resembles more that of the male parent in that the panicle is thicker and more compact than that of *B. asiatica*. For this reason the hybrid is quite ornamental; a cluster of compact pale mauve panicles presents a very attractive appearance.

The flowering period of the hybrid is also approximately intermediate between those of the parent species. Thus far the hybrid has been at its best during February and March, beginning just when *B. asiatica* is fading.

In ability to survive low temperatures the hybrid seems to be more tender than either parent. Plants of both parents and of the hybrid which were growing outdoors were subjected to a temperature of 42° F. during a night in September, 1949. Neither parent showed any injury whereas the leaves of the hybrid were black and wilted in the morning. Shortly thereafter the plants were dug up and moved into the greenhouse. One of them was killed when the temperature dropped to 50° F. one night. This plant had, of course, been weakened by recent transplanting. In general, the hybrid should be treated as *B. asiatica* with regard to protection from cold. A few cuttings have been made and rooted with a moderate degree of success. The rooting ability has not been adequately tested but it appears that cuttings will root without special difficulty.

The diploid chromosome number of both parents is 38[3]; that of the hybrid is also 38. The chromosome complements of the parents and of the hybrid are morphologically identical.

Because of the small size and rather high number of the meiotic chromosomes and the small size of the cells, it is very difficult to analyse meiotic associations of the chromosomes. So far as can be determined, the chromosomes usually seem to be associated in bivalents at metaphase I. It is not possible to state definitely that multivalents do not occur, but none has been clearly seen. Rarely a cell contains 1-2 univalents, but usually all the chromosomes are assembled in a metaphase plate which is normal in appearance. Bridges and lagging chromosomes have not been seen at anaphase. The second meiotic division also appears to present few irregularities. It appears that a high degree of homology exists between the chromosome complements of the two species.

Judging by appearance, about 10 percent of the pollen of the hybrid is normal. The plants are completely self-sterile; no enlargement of the ovary nor seed formation results from self-pollination.

Following cross-pollination between different hybrid seedlings the ovaries enlarge but no viable seed is formed. Reciprocal back-crosses to the female parent have failed to set seed.

Both the parent species are members of the section *Macrothyrsae* of the genus *Buddleja* according to the classification proposed by Bentham (see Solereder[6]). This system is based on the nature of the inflorescence and is admittedly an artificial one. No natural classification of the genus has yet been devised. Consideration of the interspecific hybridizations may provide valuable assistance in arriving at an understanding of the interrelationships of the species. *B. asiatica* and *B. japonica* are morphologically quite distinct. Both are diploid species, a fact which may indicate that they are old species, ancestral to some of the many polyploid species of east Asia. *B. asiatica* is a highly polymorphic species with a very wide distribution in central China, Burma, southern India, southeast Asia and the East Indies[2]. *B japonica* occurs in Japan and probably on the adjacent continent. At least, *B. lindleyana*, a species closely related to *B. japonica*, is widespread on the continent from central to southeast China as well as in Japan. The continuous distribution of these three species points to a

TABLE I. Comparison of hybrid with parent species.

Character	*B. asiatica*	*B. japonica*	F_1 hybrid
Corolla length	5-6 mm.	15 mm.	11 mm.
Corolla shape	straight	curved	straight
Corolla color	white	lilac	mauve (paler than *B. japonica*)
Stamen insertion	median	lower 1/3	immediately below middle
Panicle length	to 30 cm.	to 20 cm.	to 45 cm.
Flower odor	present	absent	present
Leaf shape	oblong-lanceolate	oblong-ovate	oblong-ovate
Stem	terete, not winged	square, winged	± square, not winged
Cold hardiness	tender	root-hardy	tender

close relationship; the widespread distribution may be indicative of a long existence. In view of these facts and the fact that interspecific hybridization is possible, it seems reasonable to suggest that *B. asiatica* and *B. japonica* are relatively old and closely related species.

Summary

The first generation of a hybrid between *Buddleja asiatica* Lour. (female) and *B. japonica* Hemsley is described and compared with the parent species. The chromosome number of both the parents and of the hybrid is $2n=38$.

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"BALD," A SECOND ALLELE OF HAIRLESS

In the House Mouse*

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THREE mutations causing alopecia in adult mice have been described and analyzed genetically: Naked (N)[4], hairless (hr)[1], and rhino (hr^{rh})[3], an allele of hairless. The present report describes a mutation in the mouse causing the loss of hair and resembling both hairless and rhino. The mutation was named "bald" and given the symbol "hr^{bs}" since breeding data indicated allelism with hairless.

Three bald mice, two males and one female, were noted among the litters of a breeding unit (four females and one male) of albino mice of unknown origin. Subsequent litters from the breeding unit as identified by the animal caretaker were uniformly normal. Consequently, it was not possible to reach any decisions concerning the origin of the mutation.

Homozygotes were normal in appearance until the 16th day when the hair just above the eyes and around the nose started to fall out. Heterozygous and normal mice could not be distinguished at any time. At 17-18 days, the hair on the head was thin, and at 19 days usually bald except for a few scattered hairs, a tuft of hair at each ear, and the vibrissae. The ventral area was either markedly thin or bald on the 20th day. Homozygous mice were usually completely bald within 22-28 days. According to Steinberg and Fraser[5], the pattern of hair loss in rhino is variable in that "it may range from a condition resembling the hairless pattern, with a fairly sharply defined wave of depilation progressing caudad and leaving relatively few scattered hairs in the denuded area, to a generalized thinning of hair all over the body, with the anterior-posterior gradient poorly defined (as illustrated by Howard)." Hair loss in bald mice appears to resemble rhino with some minor differences. Depilation always proceeds in a caudad direction. A gradual thinning occurs in an area before complete baldness, usually a matter of 24-48 hours, but the line of demarcation between haired and balding areas is relatively sharp.

The anterior-posterior gradient of depilation is well illustrated on the tail where hair is

*This work was supported by a contract between the University of California, Department of Bacteriology, and the Office of Naval Research, and sponsored in part by the Biological Department, Chemical Corps, Camp Detrick, Maryland.

The opinions contained in this report are not to be construed as reflecting the views of the Navy Department or the Naval Service at large.

lost progressively from the base to the tip. In some animals, a small ring of hairs may persist near the base of the tail for some time after the body has lost all hair. The legs become bald progressively but slowly so that hair may be retained on the legs longer than on any other part of the body. Vibrissae are lost after 28-30 days but shorter, curved vibrissae may sometimes appear after several weeks. Although bald mice start uniformly to lose hair on the 16th day, the rate of loss may not be the same for all animals including litter mates. Some mice retain hair up to five weeks.

Young bald mice have smooth flexible, semi-transparent skin which later becomes coarse, thickened, and opaque. Although wrinkling occurs and is most pronounced on the neck and head, the huge wrinkles or folds characteristic of rhino never develop. Obvious wrinkles on the head are evident on the 35th day. A ridge of skin develops over the eyes but vision is never completely impaired. The small, hard white lumps observed in the skin of rhino do not occur in bald. The lateral folds so characteristic of rhino are developed in bald, but not to the same degree. The nails become abnormally long and spiraled, hindering the movements of the animal. The teeth seem to be normal.

Bald mice were usually smaller than their normal litter mates when weaned. Litter mates were weighed on the 14th day before bald mice could be identified. Excepting runty normal mice, it was possible to detect bald mice by their reduced weight.

The histological details of the skin of bald mice will be the subject of a future report. One observation noted in the course of getting samples of skin should be mentioned. As in rhino, the skin was filled with vesicles containing a thick, white, pasty material.

Adult bald females have a few rudimentary nipples, but completely lack mammary tissue. Bald males and females are fertile.

Bald males were mated with normal females of the Namru strain[2]. The resulting litters were normal and contained approximately equal numbers of males and females. In the F_2 there were 130 normal and 49 bald mice. The data satisfactorily fit a monofactorial ratio. Within both categories, however, there were more females than males.

Heterozygous bald females were mated with hairless males, kindly furnished by Dr. C. C. Little, Jackson Memorial Laboratory. The litters contained 25 normal and 20 hairless mice, indicating that bald and hairless are alleles. The bald/hairless mice lost their hair according to the hairless pattern but were indistinguishable from bald mice at approximately eight weeks.

Summary

A mutation designated bald (hr^{ba}) and producing alopecia in the mouse has been described and analyzed genetically. Hairless, bald and rhino form an allelic series, recessive to normal.

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(Received November 13, 1951)

A "GINGKO LEAFED" MUTATION IN THE CUCUMBER

C. A. JOHN AND J. D. WILSON*

GINGKO-LEAF SEEDLINGS

Figure 11

The plat of seedlings shows segregation for the "gingko leaf" variation, with irregularly revolute leaves. This is a simple recessive to normal leaf form.

EARLY in the summer of 1949, an unusual segregate was observed among cucumber seedlings being grown in plant bands for ultimate transfer to the field. This segreation occurred in the F_3 of a mosaic tolerant breeding line of complicated ancestry. The immediate ancestors of this segregate were both F_2's resulting from a series of crosses and backcrosses involving National, Chinese Long, Tokyo Long Greeen, Vickery, Early Russian, Ohio 31, and an unnamed white spine slicing cucumber.

Twisted Leaves and Sterile Flowers

In Figure 11, it will be noted that the cotyledonary leaves are irregularly revolute. In Figures 11 and 12 it will be seen that all of the parts of the true leaves are much reduced except the veins which exceed the

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MATURE "GINGKO LEAF" FOLIAGE

Figure 12

Growth of gingko leaf plants is slower than of normal siblings. The tendrils are normal, but sterility is complete.

blades by an appreciable length. The leaves are scabrous, usually bipartite, rather brittle, and resemble gingko leaves to a certain extent. Growth is slower than that of normal plants during all stages and the maximum length observed was about thirty inches. Secondary runners are present but are comparatively short. Flowers of both sexes appear very late in the season and in all observations to date have been completely sterile. The incidence of flowers of both sexes was approximately normal. A very limited number of attempts at artificial pollination resulted in failure. The female ovary is shorter and thicker than the normal and is spineless. The stigma is about normal in size and the petals and sepals of the flowers of both sexes are nearly always reduced to the vascular tissue. The veins of the petals and sepals appear like tufts of very thick hairs which are covered with a downy pubescence. The tendrils are normal in length and thickness and thus are more conspicious than in the normal plant.

Hand pollinated seed from eight of the non-mutant plants was planted. Progeny from four of the plants segregated for this mutation. The combined results of this study and the application of chi square for goodness of fit to a three to one expected ratio are shown in Table I.

By applying the value (.0496) to Fisher's Tables of chi squares, it will be seen that deviations of 2.25 will occur in the somewhat over 70 percent of the trials by chance alone when the true ratio is three to one. It is concluded that this mutation is controlled by a single Mendelian recessive factor.

TABLE I. Application of Chi Square for Goodness of Fit to Observed Segregation of Normal and Gingko-Leaved Cucumber.

	Observed Frequency	Expected Frequency	Deviation	$\frac{(o-c)2}{c}$	chi Square
Normal	405	407.25	-2.25	5.0625 / 407.25	.0124
Gingko-Leaved	138	135.75	-2.25	5.0625 / 135.75	.0372
					.0496

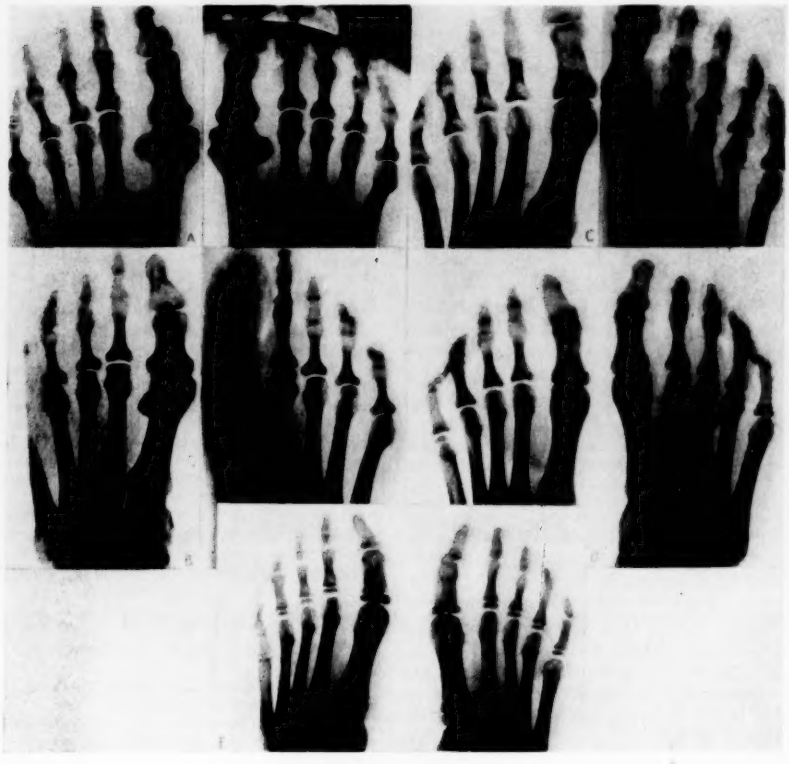
(Received August 16, 1951)

INHERITANCE OF A LONG SECOND TOE

And Short Metatarsal I Through Three Generations

TORSTEN ROMANUS

Associate Professor of Race Biology, Upsala University, Sweden.

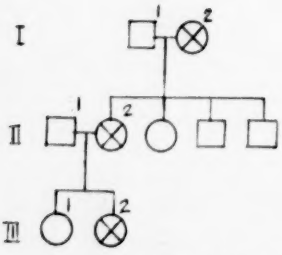


TOE "PROFILES"

Figure 13

X-ray photographs of toes of individuals in long second toe pedigree (Figure 14). Those shown are *A*—I-2; *B*—II-2; *C*—II-1; *D*—III-1; and *E*—III-2. Note that the metatarsal of the big toe of individuals shown in *A*, *B*, and *D* are short, and that this results in a relatively long second toe.

JUDGING by the few references in the literature, the possession of a second toe longer than the great toe is a character that has attracted comparatively little attention. Beers and Clark[1] have published a history of hemangioma and "short first toe" in three generations. They maintained that "short first toe" is inherited as an autosomal dominant character. Morton[2] stated that a short metatarsal I is the anatomical basis for a long second toe. Publishing radio-



TOE-LENGTH PEDIGREE

Figure 14

The three females (I-2, II-2, III-2) designated by crossed symbols have a long second toe and a short metatarsal I. (See Figure 13). II-1 has a long first toe and a long metatarsal I. (See Figure 13). The remaining individuals (I-1, II-3, 4, 5) have long first toes.

grams, he gave two cases in which both mother and daughter had a short metatarsal I. In one case (Morton[2]: Figure 81), however, the first toe was longer in both generations. The radiograms in the second case (Morton: Figure 82) provide no indication of the respective toe lengths. Part of Morton's text to Figure 81 reads: "Note that the *hypertrophy* (my italics) of metatarsal II is much greater in the older individual." The distal epicondyle of metatarsal I is usually level with or somewhat distal to metatarsal II. The distal end of metatarsal I in Morton's two cases is level with metatarsal III or IV, which usually are much shorter than metatarsal I. It would accordingly seem more correct to speak of a *short metatarsal I* rather than of a hypertrophic metatarsal II.

A paper entitled "Inheritance of Short Metatarsals" by Steggerda[4] contains a radiogram of metatarsals and phalanges. It shows, in addition to very short metatarsals IV, that metatarsals I are short and extend distally as far as metatarsals III. The illustration nevertheless reveals clearly that the great toe is longer than the second toe bilaterally.

Having studied 37 families, I have shown[3] that a long second toe is inherited dominantly but with impaired penetrance.

The pedigree here presented demonstrates a short metatarsal I combined with a long second toe through three generations. The father of I-2 reportedly had a long second toe; and so had three sisters of her seven sibs. All the three cases mentioned here concerned women (see pedigree). In generation I case 2 (Figure 13*A*) it was found that the second toe was longest—the distal end of metatarsal I was level with metatarsal III, and both these metatarsals were shorter than metatarsal IV. In case II-2, daughter of I-2, metatarsals I and III were also short and not as long as metatarsal II (Figure 13*B*). Here too the second toe was longest. Case II-1, the spouse of II-2, is included as a comparison (Figure 13*C*). In the latter case, where the great toe is longest, metatarsal I projects beyond both metatarsals II and III. In the daughters to the couple in generation II, it was found that the older (aged 11) has a longer great toe and also metatarsal I (Figure 13 *D*). The younger daughter (aged eight), case III-2, has on the other hand a longer second toe and a metatarsal I somewhat shorter than metatarsal II (Figure 13 *E*).

The pedigree shows three consecutive generations, all women, bilaterally having a long second toe and a short metatarsal I. In the family in question these anomalies are regularly inherited as dominant characters.

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THE EDITOR OF *CYTOLOGIA* DIES

To the Editor:

With great sorrow we announce the death of Dr. Kenjiro Fujii (1866-1952), Professor Emeritus of the University of Tokyo, by sudden heart failure, January 11, 1952. Dr. Fujii was also a Member of Japan Academy, Editor of the International Journal of Cytology, *Cytologia*. In 1950 he was awarded the Order of Cultural Decoration by the Emperor.

Y. Sinoto

Secretary and Publisher of Cytologia

THE INHERITANCE OF SIMPLE MUSICAL MEMORY

RICHARD ASHMAN*

THIS study of the inheritance of simple musical memory seems worth reporting since reference to the books on human heredity reveals no example of such an analysis. The trait examined is the ability to reproduce simple melodies from memory or practical absence of that ability. The family histories presented are particularly clear because of certain circumstances which will be discussed. Previous attempts to study the genetics of musical genius necessarily failed, since genius must result from fortuitous coming together of many genes, influencing different aspects of musical ability.

Beginning with generation III, brothers 5 and 6 were brought up to the ages of eight and ten, respectively, in the mountains of Virginia, with no musical contacts whatever beyond the fact that both parents could reproduce simple airs, and did so, though rarely. It is also reasonably certain that neither sib could reproduce a melody at this time. Neither had seen the inside of a school. When formal schooling and more frequent contact with music began, male 6 promptly "learned" to reproduce the simpler melodies from memory. Male 5, who is now 59 years old, has never learned. His wife, however, asserts that he can reproduce a bar or two, but never the complete melody.

More positive evidence is obtained from male 7 of generation IV. Of very good intelligence, he attended school early and was very fond of music, enjoying the school efforts to inculcate musical appreciation. At home, he liked the phonograph. By accident, he went to a college where music was stressed, and where the department of psychology, then behaviorist, regarded musical ability as an outstanding example of an acquired character! He accordingly practiced repeatedly for hours hoping to get the musical knack of reproducing a melody, but wholly without success.

Male 10 of the generation IV was encouraged by his mother to take music lessons. Although his immediate technical progress was rapid, he had no ear, and like male 7, he still has no musical memory. Male 9, however, without encouragement or training, can recall simple melodies. Male 8 showed neither interest in music nor ability, although his general intelligence is good.

Returning to the generation III, male 5 married a female with superior musical ability, whose sister, 3, is a teacher of music. Both these females and their mother have the sense of absolute pitch, according to female III-4. On a Seashore phonographic test of musical ability, taken about 27 years ago, 6 of the third generation scored 51; 5, between 15 and 20, and 3, 76. None of the sibship of female III-7 has shown musical interest, and it is likely that they all lack musical memory. Concerning the parents, nothing definite is known, but the writer's long continued contacts with them never revealed musical memory. The parents of III-5 and 6, namely II-3 and 4 definitely had musical memory. Male I-3 quite definitely lacked this ability, as his daughter frequently recalled with amusement. By implication, therefore, his wife had the ability, but this is not proven.

The mother of IV-6, says he could carry a tune, but in this instance (the mother being strongly prejudiced in favor of environment versus heredity) there may be a little doubt. One or two of the individuals of the third generation, from 8 to 13, inclusive, may possibly be wrongly classified.

The pedigree suggests that the individuals known to have had superior musical ability (II-1 and 2 and III-3 and 4) are homozygous for an incompletely dominant gene. None of the children of III-4 and 5 have shown much interest in music, and the same is true of II-3 and 4, III-6 and IV-9. Those in whom musical memory is apparently either absent or very deficient are probably homozygous recessives. It is, of course, likely that various degrees of expressivity may be found in a more elaborate study, together possibly with modifier genes.

In view of the prevalence of lack of musical memory it is doubtful whether it should be called a defect. Of particular interest is the evolutionary significance of a trait which appears to bear no relation whatever to general intelligence. Anthropologists have been criticized by geneticists for attempting to find characters of no evident survival value, positive or negative, which, therefore, might serve as suitable markers, revealing the presence in

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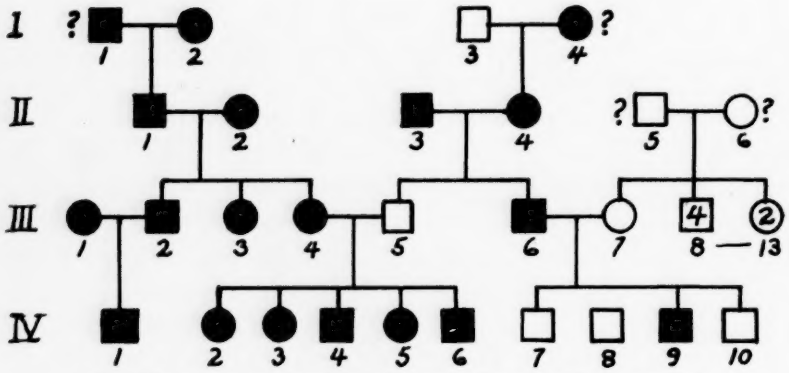

PRESENCE AND ABSENCE OF THE ABILITY TO RECALL TUNES

Figure 15

The ability to recall simple tunes is apparently not affected by environment. Individuals IV-7 and IV-10 were exposed to considerable musical training, but never learned to carry a tune. III-6, with no musical training, very quickly learned to remember melodies when he came into a musical environment.

mixture of some supposedly "primary race." Possibly musical memory is determined by a pleiotropic gene having other effects, which are of survival value. In any event, a study, not of musical ability in general, but of memory for melody, using appropriate tests, might demonstrate differences among populations, and be of value to the anthropologist.

(Received September 24, 1951)

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THE "I's"—POSITIVE OR NEGATIVE—HAVE NEED OF CORRECTION

To the Editor:

I find, unfortunately, that one sentence in my paper, "Approach to Genotypic Equilibrium —," Journal of Heredity, 42: 6: 299-300, 1951, is ambiguous.

On page 300, the text which reads "— which the heterozygote would have to lose (positive "i") or gain (negative "i"), —" would be much better in the form, "— which the heterozygote [$2q(1\text{-}q)$] would have to lose (positive "i") or gain (negative "i") *to yield the given* P_h —."

I apologize for the inconvenience caused, and request that you publish the correction.

Very truly yours,

M. J. Garber

TWO NEW HAIR MUTANTS, ROUGH AND FRIZZY

In The House Mouse*

D. S. Falconer and G. D. Snell†

TWO new mutations, rough and frizzy, affecting the structure of the hair of the mouse, were recently found, one at the Animal Breeding and Genetics Research Organization in Edinburg, the other at the Roscoe B. Jackson Memorial Laboratory in Bar Harbor. Although somewhat similar in gross appearance, tests showed the two to be genetically different.

Origin of Rough *(ro)*

This gene arose in Edinburgh in the RIII inbred strain. Its segregation was noticed when the stock was obtained from Dr. J. G. Carr in 1947, some animals having a "rough," untidy appearance of the coat. The segregation was maintained in the stock and it became evident that the "rough" coat was due to a single recessive gene, for which the name *rough*, with symbol *ro*, is proposed.

Genetics

A rough male was outcrossed to females of strain A. All the offspring were normal, confirming the supposition that rough is recessive. Two intercross matings and seven backcrosses to rough females were then made. The segregation of rough in the progeny, summarized in Table I, does not significantly disagree with expectation for a single recessive gene, though there is a considerable excess of roughs, particularly in the backcross progeny. Since both the RIII and A strains are albino, these matings gave no data on linkage with other loci. They did, however, test for linkage with sex, and it is clear from the figures in the table that there is no indication of sex-linkage.

Rough was tested for identity with the recessive waving genes, *wa-1, wa-2 we, fz,* and *fr,* by mating together homozygotes. In each case only normal offspring were obtained; rough is therefore not identical with any of these genes.

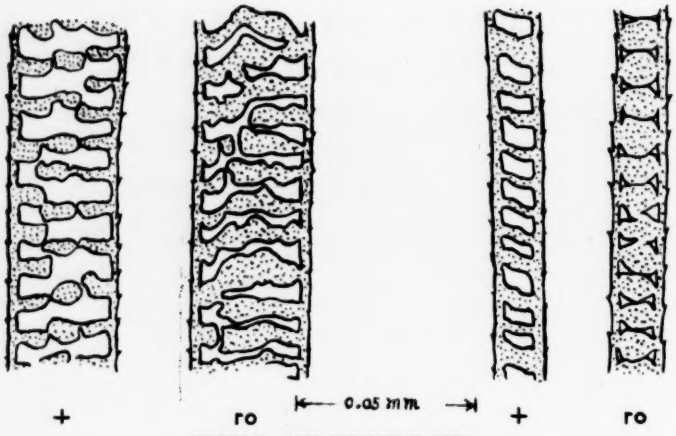
Description

The most reliable characteristic for the classification of rough homozygotes is the waving of the vibrissae. This is apparent a few days after birth and, though reduced, is still visible in the adult. Between one and two weeks of age the waving of the whiskers is as fully pronounced as that of waved-*2* or wellhaarig mice, but in the adult it is less extreme. Comparison of the degree of waving with that of the other waving genes cannot, however, be made with confidence since rough has only been observed on the background of the RIII strain.

The hairs of the coat are not waved, and the appearance of the coat in no way resembles that of the other waving genes. In albino mice the general appearance is one of untidiness, the hairs tending to stick together in bundles as if the coat were wet or greasy, and the shade of white is less pure. (The effect of the gene on colored coats has not yet been observed.) Microscopic examination of the hairs revealed two abnormalities in homozygotes when compared with heterozygous litter-mates. First, the septa between the air-spaces are generally thicker, and the air-

*The work on frizzy was supported in part by a research grant from the National Cancer Institute, of the National Institutes of Health, Public Health Service. The authors wish to acknowledge the kind assistance of Miss Margaret Dickie and Miss Elizabeth Fekete in carrying out the study of the hair and skin structure of frizzy mice and of Mr. Frederick Gabrielson in carrying out the breeding tests with this mutation.

†Animal Breeding and Genetics Research Organization, Edinburgh, Scotland, and Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine.



NORMAL AND ROUGH HAIRS

Figure 16

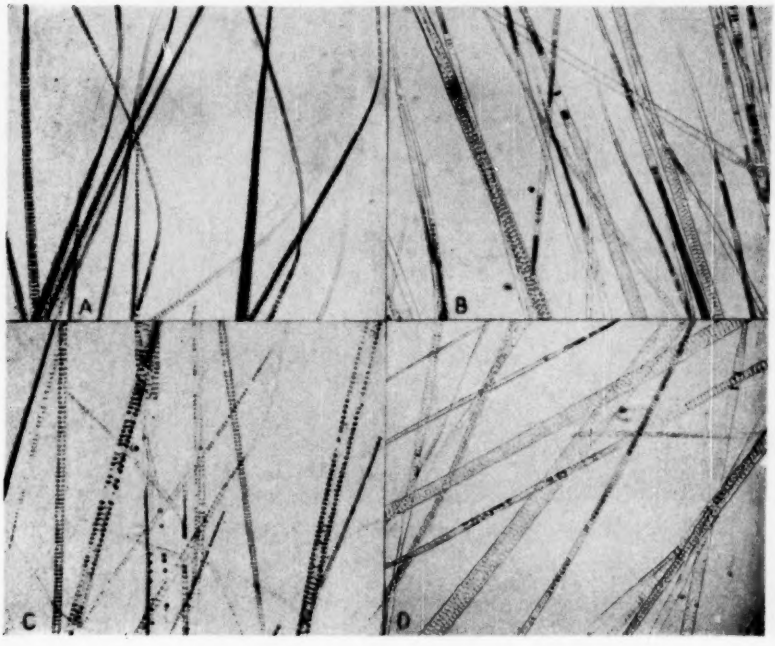
Camera lucida drawings of normal (+) and rough hairs (*ro*) under high magnification with the air-spaces filled with water. Awl-type hair is shown on the left and zigzag hair on the right.

spaces consequently smaller. Individual hairs vary somewhat in this abnormality, and the hairs illustrated in Figure 16 were chosen as being typical of the samples examined. Secondly, more than half of the air-spaces of rough hairs do not contain air, but are filled with fluid. Typical samples of normal and rough hairs are illustrated in Figure 17*A* and *B*. These hairs were mounted in Canada balsam without any previous treatment. This lack of air in the hairs clearly accounts for the "off-white" appearance of the coat.

That the fluid-filled spaces in the hairs contain water which fails to dry out is suggested by the following observations. When normal hairs are immersed in water which is not saturated with air, the air in the hairs dissolves out and is replaced by water. Water will not displace the air by capillarity, but only when the air is removed by solution. If the hairs are then allowed to dry, air re-enters the hairs, displacing the water, as soon as the surface of the hair has dried. The re-entry of the air is very rapid, but if a drop of Canada balsam is placed on the sample of hairs at the critical moment and the entry of air is stopped when some of the air-spaces are filled with air and the rest with water, the appearance of rough hairs is reproduced. Rough hairs treated in the same manner behave in exactly the same way, and when the air has been replaced by water no difference can be seen, even with a high magnification, between the originally fluid-filled spaces and the spaces which are known to contain water. When the rough hairs are then allowed to dry, air does not enter the spaces that were originally fluid-filled, even when the hairs are dried for a day over phosphorous pentoxide. The cause of the fluid failing to escape from these spaces seems to be the extra greasiness of the surface of the hair, because if rough hairs are first washed in ether and then dessicated, a much larger proportion of the air-spaces are found to be air-filled. This observation is illustrated in Figure 17*C* and *D*, which shows two samples of rough hairs from the same animal, both dried for a day over phosphorous pentoxide, but one of which, *C*, had been previously washed for a day in ether. Finally, if dead rough mice are thoroughly washed with ether and then allowed to dry the characteristic appearance of the coat largely disappears and the mice become almost indistinguishable from normals. It is therefore clear that the general appearance of the rough coat is also caused by the extra greasiness of the hairs.

Origin of Frizzy *(fr)*

The mutation "frizzy" first appeared in June, 1949, at the Jackson Laboratory in a pink-eye chinchilla shaker-1 stock. This stock was of mixed origin, having come from a cross between strain DBA and a pink-eye chinchilla shaker-1 strain carrying the *T(1;?)c* translocation. Tests showed the mutation to be a simple Mendelian recessive. It is proposed



AIR SPACES IN NORMAL AND ROUGH HAIR

Figure 17

Photomicrographs of samples of normal and rough hairs mounted in Canada balsam. *A*—normal; *B*, *C*, *D*—rough. *A* and *B* are untreated; *C* and *D* are dessicated. *C* was previously treated with ether. Air-filled spaces appear black.

that it be assigned the symbol *fr*.

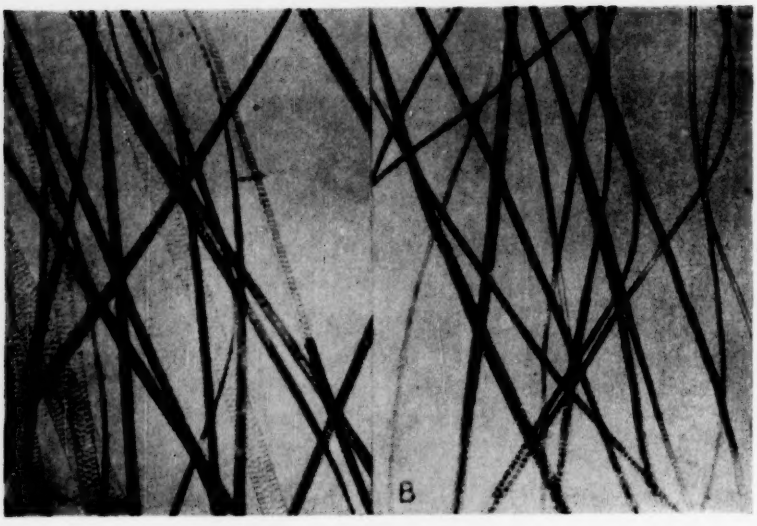
Frizzy mice can be identified at one to two days after birth by the wavy or curly appearance of the vibrissae. The waviness persists throughout life and is the easiest method of recognizing affected animals. As the coat grows in, it appears somewhat short and rough, and at about two weeks many show slight waviness. Mice of six to seven weeks, which have undergone the first moult, may appear almost normal except for the vibrissae, but in older animals the coat almost always appears short and thin. The degree of expression is probably subject to considerable modification in different genetic backgrounds; however, there is no indication that normal overlaps occur.

Examination of the hairs showed that while all four types described by Dry[2] (see also Dickie and Woolley[1],) are present, there is a poucity of the heavier or coarser categories (monotrichs, awls and auchenes). The great bulk of the hairs are of the fine, "zigzag" type. While we have not made measurements, we get the impression also that the hairs of each type are on the average more slender than normal. Typical examples of normal and frizzy hairs are shown in Figure 18.

Frizzy mice of four days of age sometimes show a scaliness of the skin of the tail. Small swellings may be present. Examination of histological sections shows this condition to be due to local thickenings of the cuticle.

Genetics and Linkage

Since the characteristic appearance of frizzy mice is somewhat unlike that of any of the previously described mutations affecting the pelage, it seemed unlikely that it was allelic with any of them. However, it was tested by crossing to *fz*, *wa-1* *wa-2* and, as already mentioned, to *ro*. First generation hybrids were normal in every case. Thereafter the discovery of a linkage locating *fr* in a



NORMAL AND "FRIZZY" HAIR

Figure 18

A—Hair of normal mouse about six months old (×96). The light color of the large hairs (awls) is due to penetration of the air spaces by the mounting medium. *B*—Hair of frizzy mouse about six months old. (×96). Note absence of the large "awls." These however are found occasionally, though in most animals the proportion is very low. Note also that the "zigzags," characterized by a single row of air spaces, are in general more slender than in the normal.

chromosome area free of any other known mutations affecting coat structure made further tests unnecessary.

By a happy coincidence, *fr*, which appeared in a stock carrying the first chromosome genes *p*, c^{ch} and *sh-1*, turned out to lie on the first chromosome. While some other linkage crosses were started, they were discontinued as soon as this linkage was found.

The linkage data with *p*, c^{ch} and *sh-1* are given in Table II. Some of the animals came from a cross which was segregating for *Wh*. Since there is a possibility that this may have caused confusion in the classification of chinchilla (c^{ch}), animals from this cross are given separately. The apparent crossing over between c^{ch} and *sh-1* is rather high in this group.

The data show the order of the genes to be *p* c^{ch} *sh-1* *fr*. It is notable that there were no double crossovers even between *p* and *fr*. Grüneberg[3] found only five double crossovers between *p* and *sh-1* out of a total of 2188 backcross mice from heterozygous females, and zero out of 946 among mice from heterozygous males. It is thus not surprising that we found none in this interval with our more limited data, but the chance of double

TABLE I. Segregation of rough.

	rf ♀♀	*rf* ♂♂	+ ♀♀	+ ♂♂
Backcrosses	32	38	24	26
Intercrosses	12	17	34	23

TABLE III. Crossover percents between different first chromosome marker genes, based on data in Table II.

	p - c^{ch}	c^{ch} - *sh-1*	*sh-1* - *fr*
♀ heterozygous	11.4 ± 4.1%	8.1 ± 4.1%	15.4 ± 4.1%
♂ heterozygous	8.2 ± 6.4%	1.6 ± 6.4%	16.4 ± 6.4%

TABLE II. Data from cross *p* c^{ch} *sh-1* *fr*/+ + + + × *p* c^{ch} *sh-1* *fr*/*p* c^{ch} *sh-1* *fr*, proving location of *fr* on first chromosome. No double or triple crossovers were found; hence these classes are omitted.

	+ + +	*p* + +	*p* c^{ch} +	*p* c^{ch} *sh-1*	*p* c^{ch} *sh-1* *fr*	+ + *fr*	+ c^{ch} *fr*	+ *sh-1* *fr*	+ + *fr*	total
♀ heterozygous										
Wh not present	39	6	3	9	25	4	3	6	95	
Wh present	22	5	6	7	11	2	0	1	54	
♂ heterozygous										
Wh not present	15	1	0	4	11	1	1	3	36	
Wh present	18	2	0	3	1	1	0	0	25	

crossovers in the longer *p-fr* interval should be considerably increased.

Table III shows the crossover values for the three different segments. The crossing over between *sh-1* and *fr* was 15.4 ± 4.1 percent when the female was the heterozygous parent, 16.4 ±6.4 percent when the male was the heterozygous parent.

It is apparent from Table II that there is a deficiency of frizzies as compared with the expected 1:1 ratio. Where *Wh* was not involved in the cross, the ratio of non-frizzy to frizzy was 77 to 54. In the crosses segregating for *Wh* the ratio was 63 to 16. This deficiency of *fr* is probably due in part to a lowered viability of frizzy homozygotes and in part to the fact that *fr* was coupled with *sh-1* which also may lower viability. The reason for the great deficiency in the crosses with *Wh* is not clear. Our records show 15.2 percent mortality between first and final observation of the litter for crosses with *Wh* and 12.1 percent for crosses without. This difference is so slight that it cannot explain the deficiency; if there was unusual mortality of frizzy homozygotes in the *Wh* crosses it must have taken place prior to the first check of the litters which was routinely made at one to seven days. Some of the litters were recorded during a period when the loss of young mice in our colony was unusually high, and there may have been a disproportionate number weaned from the *Wh* group during this interval.

The breeding of the pink-eye chinchilla shaker-1 frizzy stock is as satisfactory as that of most multiple factor stocks.

Summary

Rough (*ro*) is a new recessive gene of the house mouse which segregates normally and independently of sex. In homozygotes the vibrissae are waved in the manner of the previously known waving genes, but the hairs of the coat are not waved. The general appearance of the coat is one of untidiness and the color of albinos is slightly "off-white." The hairs have thickened internal septa and reduced air-spaces, more than half of which contain fluid instead of air. In addition the hairs are greasier than those of normals.

Frizzy (*fr*) is a new recessive mutation in the mouse in which the vibrissae are curled and the structure of the coat is altered by a decrease in the proportion of the coarser types of hairs. The cuticle on the tail may show abnormalities in mice of about four days of age.

Frizzy lies on the first chromosome, the order of the genes being *p* c^{ch} *sh-1 fr*. The percent of crossing over between *sh-1* and *fr* was 15.4 ± 4.1 when the female was the heterozygous parent and 16.4 ± 6.4 when the male was the heterozygous parent.

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2. Dry, F. W. *Jour. Genetics* 16:286-340. 1926.

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ABNORMAL PETIOLE AND PETIOLULE DEVELOPMENT IN RED CLOVER

Trifolium pratense L.

A. A. Hanson and R. G. Hanson*

. LONG PETIOLULES

Figure 19

Abnormal red clover plant typical of group (i). Elongated petiolules and reduced petioles create impression that plant is unifoliate. ¾×.

IN the fall of 1950, 28 abnormal seedlings were observed in an F_1 population of 266 red clover plants. The two parental clones had survived successive greenhouse inoculations of *Sclerotinia trifoliorum* Eriks., and had been crossed under cages with bumble bees in the spring of 1950. The abnormal plants were characterized either by the absence or near absence of petioles, and by leaflets in which the central petiolule was appreciably longer than the lateral ones. The petiolules were greatly elongated as contrasted with the normal type. The leaves that did not have a normal petiole maintained the trifoliolate

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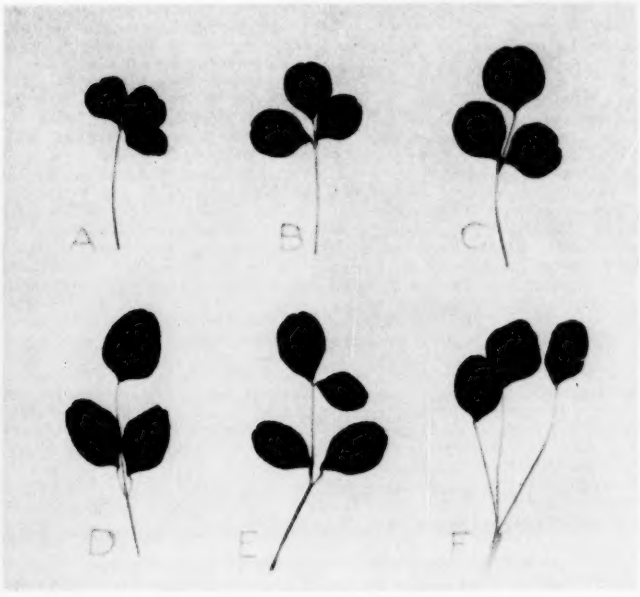

NORMAL AND VARIANT LEAVES

Figure 20

Basal leaves from mature plants: *A*—Normal red clover leaf; *B-E* show variations in petiolule development typical of phenotype group (ii). *F*—shows reduced petiole and elongated petiolules present in group (i). Approximately ½×.

condition, as the petiolules were joined just below or near the apex of the stipules. In the seedling stage the abnormal plants produced a larger rosette and were much shorter than the normal types.

The two parental clones together with abnormal and normal "F_1" plants, and unrelated normal plants, were brought into the greenhouse for observation and crossing. Somatic chromosome counts revealed a normal chromosome complement ($2n = 14$) and no obvious change in chromosome morphology. When the plants were placed under 15-hour days it was observed that height and number of stems, number of flowers, flowering and seed production, were apparently normal. As the plants matured, considerable variation occurred in the expression of the abnormal character. In general, the abnormal plants consisted of: 20 plants with elongated petiolules and reduced petioles (Figures 19 and 20 *F*); and eight plants with lateral petiolules much shorter than the central one. All of the leaves of this second group had petioles, and at least half of the leaves were normal (Figure 20 *A-E*).

The "F_1," "F_2" and "first backcross" generations, together with test crosses were produced by hand pollination. The parental clones proved to be completely self-sterile. Seed resulting from the above crosses were planted in flats in August 1951, and the progenies classified at the seedling stage.

In contrast with the original "F_1", which segregated, 28 abnormal: 238 normal, no abnormal seedlings were observed in a second population of 435 "F_1" seedlings. The original cross was made with bees in June while the

second hybrid population resulted from crosses made by hand in January and February.

The behavior of the remaining populations are shown in Table I. No abnormal plants were obtained when normal "F_1" plants were used to produce the "F_2" generation, the first backcross generation to the original parents, or outcrosses to unrelated normal plants. On the other hand, the "F_2" populations produced from abnormal parents gave either 3:1 or 1:1 ratios for abnormal vs. normal types. The abnormal parents could be differentiated into two classes on the basis of genetic behavior—an Ab_A class which when intercrossed gave 3:1 ratios for abnormal and normal types; and an Ab_B class which gave 1:1 ratios when crossed with plants classified as Ab_A, or 3:1 ratios when intercrossed. These two classes were not closely associated with the arbitrary phenotypic groups described previously. The two abnormal classes gave similar results, both when backcrossed to the original parents and when crossed with unrelated normal plants. The progenies did not deviate significantly from a 1:1 ratio for abnormal vs. normal types. The cross $Ab_A \times N$ had a total chi-square which approached the five percent level of significance, while the heterogeneity chi-square was significant at the five percent point. The results reported in Table I show that this discrepancy can be accounted for by one family which segregated, 53 abnormal: 25 normal.

The data suggest that complementary factors govern the expression of normal petioles and petiolules. When dominant alleles, *A* and *B*, of both these factors are present, a normal phenotype results. The absence of one or the other produces abnormal types. Apparently the expressions of the abnormal phenotype is partially governed by one or more modifying factors. This hypothesis will account for the above results provided the original parents were homozygous recessive, and that either (a) the abnormal plants resulted from pollen contamination, or (b) two somatic mutations occurred in the original parents, and the stem or stems were lost when the parents were increased vegetatively for further crossing.

Plants with multiple leaflets are not uncommon in the genus *Trifolium*. Atwood[1] has reported a unifoliate type in white clover. No references were found that mention abnormal red clover plants similar to those discussed in this paper.

Literature Cited

1. Atwood, Sanford S. *Jour. Hered.* 29: 239-240. 1938.

TABLE I. Summary of F_2, backcross and test cross segregations.

Source*	No. of Families	No. of Plants	Abnormal Plants Observed No.	Abnormal Plants Expected No.	Total X^2	Total P	Pooled X^2	Pooled P	Heterogeneity X^2	Heterogeneity P
F_2 GENERATION										
$Ab_A \times Ab_A$	12	434	113	325.5	9.89	0.5-0.7	1.92	0.1-0.2	7.97	0.7-0.8
$Ab_A \times Ab_B$	6	230	125	115.0	3.03	0.8-0.9	1.74	0.1-0.2	1.30	0.9-0.95
$Ab_B \times Ab_B$	1	82	62	61.5	0.02	0.8-0.9	-	-	-	-
$Ab_A \times N$	9	540	275	270.0	15.92	0.05-0.1	0.19	0.5-0.7	15.73	0.02-0.05
$Ab_A \times N$†	8	462	222	231.0	5.18	0.7-0.8	0.70	0.3-0.5	4.48	0.7-0.8
$Ab_B \times N$	2	131	61	65.5	1.12	0.5-0.7	0.62	0.3-0.5	0.50	0.3-0.5
$N \times N$	1	70	0	0.0	-	-	-	-	-	-
BACKCROSS GENERATION										
$Ab_A \times P_1$	13	583	284	291.5	15.50	0.2-0.3	0.39	0.5-0.7	15.11	0.2-0.3
$Ab_A \times P_2$	8	324	156	162.0	6.22	0.5-0.7	0.44	0.5-0.7	5.78	0.5-0.7
$Ab_B \times P_2$	2	64	28	32.0	1.67	0.3-0.5	1.00	0.3-0.5	0.67	0.3-0.5
$N \times P_1$	4	262	0	0.0	-	-	-	-	-	-
$N \times P_2$	4	145	0	0.0	-	-	-	-	-	-
TEST CROSSES										
$Ab_A \times UN$	7	152	68	76.0	4.84	0.5-0.7	1.68	0.1-0.2	3.16	0.7-0.8
$Ab_B \times UN$	4	103	50	51.5	5.99	0.1-0.2	0.09	0.7-0.8	5.90	0.1-0.2
$N \times UN$	4	242	0	0.0	-	-	-	-	-	-

*Ab_A and Ab_B = abnormal F_1 plants distinguished by their behavior when intercrossed; N = normal F_1 plants; UN = unrelated normal plants; P_1 and P_2 = parental clones.

†Omitting one family which segregated, 53 abnormal: 25 normal.

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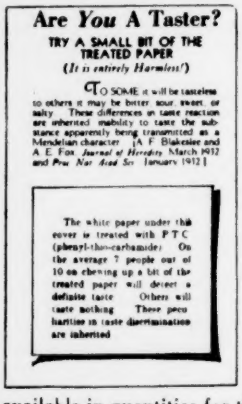
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